

Geospatial modeling in marine recreational fisheries science

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PhD Thesis

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Als meus pares

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Abbreviations and acronyms

ACI	average covering index
AIC	Akaike information criterion
AMDB	angler monitoring database
AUC	area under the curve
BBCA	Braun-Blanquet cover abundance
BRT	boosted regression tree
BZ	buffer zone
CWT	continuous wavelet transform
CI	credible intervals
COA	centre of activity
CPUE	catch per unit effort
CV	cross-validation
DBM	digital bathymetric model
DIC	deviance information criterion
DSS	decision support system
EAF	ecosystem approach to fisheries
EBM	ecosystem-based management
EROS	Earth Resources Observation and Science
FAO	Food and Agriculture Organization of the United Nations
GIS	geographic information system
GLM	generalized lineal model
GLMM	generalized lineal mixed model
GPS	global positioning system
ICM	integrated coastal management
IMP	integrated maritime policy
IOR	index of reuse
IUCN	international union for conservation of nature and natural resources
IZ	integral zone
KUD	kernel utilization distribution
MBA	multilevel B-spline approximation
MCA	multi-criteria analysis
MCMC	Markov Chain Monte Carlo
MCP	minimum convex polygon
MPA	marine protected area
MS222	tricaine methanosulfate
MSFD	marine strategy framework directive
MSP	marine spatial planning
PBMR	Palma Bay marine reserve
PCA	principal component analysis
PPUE	price per unit effort
RC	relative contribution
REML	restricted maximum likelihood
RMSE	root mean square error
SA	spatial autocorrelation
SCI	site of community importance
SDM	species distribution model
SSS	side scan sonar
SST	sea surface temperature
TL	total length
UD	utilization distribution
UTM	universal transverse Mercator
VIF	variance inflation factor
WRT	water residence time
YPUE	yield per unit effort

Abstract

In Mediterranean marine ecosystems, fishing effort is shifting from small-scale commercial fisheries towards recreational fishing. Recent works have demonstrated that the impact of recreational fisheries is not negligible and that such complex socio-ecological systems should be taken into account under the widely proposed ecosystem-based approach. The ecosystem approach to fisheries takes into consideration the interaction between biotic, abiotic and human components; and depends on a deeper understanding on the fine-scale patterns of exploitation. Spatial dimension of fisheries plays a key role on resource sustainability by determining the spatial structure of exploited fish populations and the spatial allocation of fishing effort. However, spatial dimension of fisheries is frequently ignored because usually demands sophisticated approaches and technology suited to obtain fine-scale position data of fish and anglers.

This thesis proposes different geospatial approaches for assessing the spatial dimension of the coastal recreational fisheries using quantitative methods and computational tools. Spatial information on benthic habitats, fish mobility and fishing quality were combined for estimating fishing effort and harvest using an original spatially-explicit approach. The aim is to advance in our understanding of angler spatial behaviour using a holistic approach based on empirical data and statistical models. In order to illustrate the proposed framework, the 'roquer' modality, one of the most popular coastal recreational fisheries in the Mediterranean Sea, was used as case study at Palma Bay (NW Mediterranean).

A drop-camera system was designed and developed to monitor shallow (i.e., up to 40 m depth) benthic habitats at large (i.e., 100 km^2) spatial scales. Underwater images together with spatial models of biophysical variables and geospatial models provided valuable information for assessing the distribution of seagrass meadows of *Posidonia oceanica*.

Fish movements of two of the main target species, *Serranus scriba* and *Diplodus annularis*, were examined using acoustic telemetry and external tagging in a marine protected area (MPA) mainly dominated by *P. oceanica*. Results highlight small home range sizes and high site fidelity of those species, thus supporting that they could be used as reliable bioindicators of local-scale patterns of fishing exploitation.

Fishing-catch variables, here referred as fishing quality, were analysed based on experimental angling sessions and biophysical variables. Results demonstrated that fishing quality is a function of environmental conditions together with angler-related factors like angler experience or bait type. Considering the reduced home range sizes of the species, spatial predictions of different fishing quality metrics were conducted across Palma Bay. Those metrics were then used for assessing the spatial distribution of fishing effort. In combination with other attributes that affected angler site allocation, like weather conditions or accessibility, a predictive model was developed using machine-learning tools. Complex responses like non-linearities, interactions and threshold effects were taken into account for predicting fishing effort. Finally fishing effort calculations were combined with the model of fishing quality (i.e., yield) to provide estimates of total fishing harvest and its uncertainty. Interestingly, results clearly indicate that fishing effort and harvest are spatially heterogeneous, thus supporting that the naïve assumption of homogeneous distribution can severely affect accuracy and precision, thus compromising stock sustainability.

This thesis demonstrates how knowledge on spatial distributions of biotic, abiotic and human components can be used for better understanding of complex socio-ecological systems and supports the implementation of the principles of the ecosystem approach to fisheries management.

Resumen

El esfuerzo pesquero en los ecosistemas marinos Mediterráneos está registrando un cambio sustancial, pasando de la pesca comercial de pequeña escala a la pesca recreativa. Trabajos recientes han mostrado que el impacto de la pesca recreativa no es insignificante y que estos complejos sistemas socioecológicos deben ser considerados en el marco del enfoque ecosistémico. El enfoque ecosistémico de la pesca tiene en cuenta la interacción entre aspectos bióticos, abióticos y humanos; y se basa en una comprensión profunda los patrones de explotación de pequeña escala. La dimensión espacial de la pesca juega un papel clave en la sostenibilidad de los recursos, permitiendo la caracterización de la estructura espacial de las poblaciones de peces explotadas y de la distribución espacial del esfuerzo pesquero. Sin embargo, este componente espacial de las pesquerías no suele ser tenido en cuenta, al necesitar de enfoques sofisticados y tecnología adecuada para obtener datos de posición precisos de peces y pescadores.

El presente trabajo de tesis doctoral propone diferentes enfoques geoespaciales destinados al análisis de la dimensión espacial de las pesquerías recreativas costeras utilizando métodos cuantitativos y herramientas computacionales. Diferentes tipos de información espacial, relativas a los hábitats bentónicos así como a la movilidad y a la calidad de las capturas, han sido combinadas para estimar el esfuerzo de pesca y las capturas totales, utilizando un enfoque original y espacialmente explícito. El objetivo es el de progresar en la comprensión del comportamiento espacial del pescador a través de un enfoque holístico basado en datos empíricos y modelos estadísticos. La modalidad de pesca del 'roquer', una de las pesquerías recreativas costeras más populares en el Mediterráneo, ha sido utilizada como caso de estudio en la bahía de Palma (en el Mediterráneo noroccidental).

Un sistema de cámara submarina remota fue diseñado y puesto en marcha para llevar a cabo un seguimiento de los hábitats bentónicos en zonas poco profundas (de hasta 40 m de profundidad) en una gran extensión (100 km^2). Las imágenes submarinas resultantes, juntamente con los modelos espaciales de las variables biofísicas y los modelos geoespaciales, proporcionaron una valiosa información que permitió evaluar la distribución de las praderas de *Posidonia oceanica*.

El movimiento de los peces de dos de las principales especies objetivo de la pesca recreativa, *Serranus scriba* y *Diplodus annularis*, fue examinado mediante técnicas de telemetría acústica y de marcaje externo en un área marina protegida (AMP) dominada principalmente por *P. oceanica*. Los resultados destacan un tamaño reducido de área de campeo y una elevada fidelidad al sitio de estas especies, justificando así su utilización como bioindicadores fiables de los patrones de explotación pesquera de pequeña escala.

Las variables de capturabilidad, aquí señaladas como variables de calidad de pesca, fueron analizadas mediante sesiones de pesca con caña experimentales y variables biofísicas. Los resultados demostraron que la calidad de la pesca es una función de las condiciones ambientales y de factores relacionados con el pescador, como la experiencia o el tipo de cebo utilizado. Teniendo en cuenta el reducido tamaño del área de campeo de la especie, se realizaron predicciones espaciales de diferentes indicadores relativos a la calidad de la pesca en la bahía de Palma. Dichos indicadores fueron a su vez utilizados para evaluar la distribución espacial del esfuerzo pesquero. Combinado con otros factores que contribuyen a la elección del emplazamiento del pescador, como son las condiciones meteorológicas o la accesibilidad del lugar, un

modelo predictivo fue desarrollado mediante algoritmos de aprendizaje automático. Respuestas de elevada complejidad, como la no-linealidad, las interacciones y los efectos umbral, fueron consideradas para predecir el esfuerzo de pesca. Finalmente, los cálculos relativos al esfuerzo de pesca fueron combinados con el modelo de calidad de la pesca (el peso de las capturas) para proporcionar estimaciones de las capturas totales de pesca y de la incertidumbre asociada. Resulta interesante comprobar que los resultados indican claramente que el esfuerzo de pesca y las capturas totales son espacialmente heterogéneas. Este hecho evidencia que una suposición "naive" de distribución homogénea puede afectar gravemente a la exactitud y a la precisión de las capturas, comprometiendo así la sostenibilidad de los stocks de peces.

En esta tesis se pone de manifiesto la manera cómo el conocimiento sobre la distribución de los componentes bióticos, abióticos y humanos puede ser utilizado para una mejor comprensión de los complejo sistemas socioecológicos, permitiendo así la aplicación de los principios del enfoque ecosistémico a la gestión de los recursos pesqueros.

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List of publications

The contents of this thesis have derived into different articles published in international journals, where I have been the lead author. Writing this dissertation would not have been possible without the help of my colleagues. For that reason, and as grateful to all of them, I have written the Chapters in plural form.

March, D., J. Alós, M. Cabanellas-Reboredo, E. Infantes, and M. Palmer. 2013b. Probabilistic mapping of *Posidonia oceanica* cover: A Bayesian geostatistical analysis of seabed images. Aquatic Botany 106:14-19. (Chapter 2)

March, D., J. Alós, M. Cabanellas-Reboredo, E. Infantes, A. Jordi, and M. Palmer. 2013a. A bayesian spatial approach for predicting seagrass occurrence. Estuarine, Coastal and Shelf Science 131:206-212. (Chapter 3)

March, D., M. Palmer, J. Alós, A. Grau, and F. Cardona. 2010. Short-term residence, home range size and diel patterns of the painted comber *Serranus scriba* in a temperate marine reserve. Marine Ecology Progress Series 400:195-206. (Chapter 4)

March, D., J. Alós, A. Grau, and M. Palmer. 2011. Short-term residence and movement patterns of the annular seabream *Diplodus annularis* in a temperate marine reserve. Estuarine Coastal and Shelf Science 92:581-587. (Chapter 5)

March, D., J. Alós, and M. Palmer. 2014. Geospatial assessment of fishing quality considering environmental and angler-related factors. Fisheries Research 154:63-72. (Chapter 6)

March, D., J. Alós, R. Arlinghaus, and M. Palmer. Spatio-temporal patterns of fishing effort and total harvest in marine recreational fisheries. In prep. (Chapter 7)

SECTION I. INTRODUCTION

Chapter 1
Introduction

1.1 Ecosystem approach to fisheries

Across the globe, human activities are increasing in presence and impact on the oceans and nearshore ecosystems (Halpern et al. 2008, Halpern et al. 2012). The sustainable development of such activities has been acknowledged as a major challenge at the global scale, and incorporated into international actions (e.g., Assessment 2005, UN 2012). In Europe, the long term strategy to support sustainable development of maritime activities is referred as Blue Growth (EC 2012). This strategy is based on an integrated management of human activities and marine resources under the Integrated Maritime Policy (IMP). On the one hand, IMP considers the interactions among human activities and can be supported by the implementation of marine spatial planning (MSP), which can be considered as "a process of public authorities of analyzing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic and social objectives" (Ehler and Douvere 2009). The implementation of MSP is aimed at ensuring an efficient management of activities at sea. On the other hand, IMP not only considers interactions between activities but also the interactions of human activities with the environment and natural resources. Under the environmental pillar of the IMP is the Marine Strategy Framework Directive (MSFD; EC 2008), which emphasizes the use of holistic approaches, such as the ecosystem-based management (EBM; Arkema et al. 2006). In recent years, an increasing number of terms, concepts and implementations of EBM have been identified (Arkema et al. 2006, Levin et al. 2009, Essington and Punt 2011), however EBM can be understood as an integrated approach that considers the entire ecosystem, including humans, with the aim of reaching a trade-off between ecosystem health and human well-being (Leslie and McLeod 2007). In fact, EBM has emerged to a central paradigm underlying living marine resource policy (Leslie and McLeod 2007, Levin et al. 2009).

Fisheries, whether commercial or recreational, constitute a maritime activity of major concern in both socio-economic terms and environmental impacts. The management of fisheries has evolved during the last decade into the concept of EBM as well (Essington and Punt 2011). At the EU level, EBM is considered under the umbrella of the Common Fisheries Policy (CFP; EC 2013a), and it is referred as ecosystem approach to fisheries (EAF; Garcia and Cochrane 2005, Jennings and Rice 2011). Following FAO (2003), "an ecosystem approach to fisheries strives to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying and integrated approach to fisheries within ecologically meaningful boundaries".

EAF of nearshore ecosystems depends on a deeper understanding of fine-scale patterns of exploitation (Crowder et al. 2008, Parnell et al. 2010), while the spatial dimension of fisheries plays a key role in resource sustainability by determining the spatial structure of exploited fish populations and the spatial allocation of fishing effort (Lorenzen et al. 2010). In particular, spatial information regarding fishing effort

and fishery resources is important for understanding angler behaviour, for supporting fisheries management (Norse 2010, Hunt et al. 2011, Fenichel et al. 2012, Post and Parkinson 2012) and for proper design of marine spatial planning (MSP; Foley et al. 2010, Rassweiler et al. 2014). Especially important for spatial management of fisheries are the knowledge on spatial components of the ecosystem, like habitats, and a better understanding of key processes like fish movements.

The identification of Essential Fish Habitats (EFH), i.e. areas or volumes of water and bottom substrates that provide the most favourable habitats for fish populations to spawn, feed and mature throughout their full life cycle, is important for the spatial management of fisheries (Rosenberg et al. 2000). EFH analysis considers the relationships between fish and the environment. In regard to this point, the spatio-temporal variability of marine ecosystems presents a major challenge for EFH analysis. For pelagic and more mobile fish species, oceanographic conditions like sea surface temperature (SST) or chlorophyll-a (Chl-a), are usually considered as habitat descriptors (Bellido et al. 2008, Valavanis et al. 2008). In contrast, for demersal fisheries and less mobile species, benthic habitat type is an important factor affecting the spatial distribution of fish (Garcia-Charton et al. 2004, Crec'hriou et al. 2008). Spatial patterns in seafloor structures determine where fish feed and spawn (Norse 2010). Therefore habitat heterogeneity can be considered as one of the main determinants of the spatial structure of demersal fisheries (Letourneur et al. 2003, Stobart et al. 2012).

Fish movements have consequences for spatial management of fisheries as well. The spatio-temporal behaviour of fish is relevant to a number of marine management and conservation issues (Pittman and McAlpine 2003, Botsford et al. 2009). For example, fish movements and home range sizes are important factors to consider in the design of marine protected areas (MPAs), as the benefits of a marine reserve have been shown to be dependent upon the rate and scale of movement of species in relation to the reserve size (Kramer and Chapman 1999, Sale et al. 2005). To provide effective protection, MPAs must be large enough to enclose the appropriate habitats, to contain regular movements of target species (i.e., their home range), but also to allow dispersal and cross-boundary movements from adults or early life stages to fishing grounds (i.e., spillover; Kramer and Chapman 1999, Bartholomew et al. 2008). In addition, quantification of home range sizes and site fidelity is relevant for considering the use of fish species as bioindicators of human impacts. In this regard, sedentary species are more suitable for representing local exposure to human impacts and assessing ecosystem health (Burger and Gochfeld 2001).

In Mediterranean coastal ecosystems, fishing effort is shifting from small-scale commercial fisheries towards recreational activity (Morales-Nin et al. 2010). For example, the evolution of the number of fishing permits issued in Balearic Islands shows an increasing trend (Figure 1.1), while commercial landings have remained stable (Morales-Nin et al. 2010). Relative to the effects of commercial fishing, the potential impacts of recreational fisheries on fish stocks have traditionally been consid-

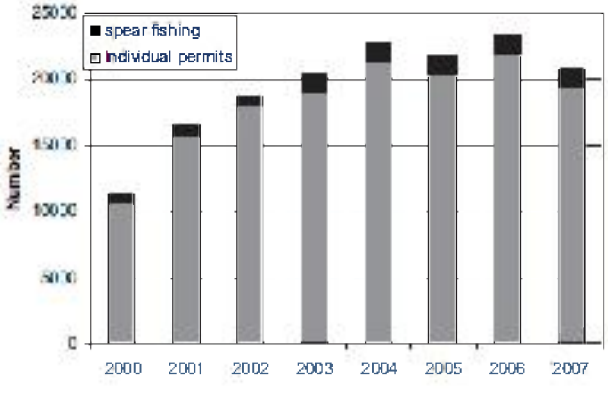


Figure 1.1 Evolution of the number of recreational fishing permits for spear divers and anglers. Reproduced from Morales-Nin et al. (2010)

ered negligible (Cooke and Cowx 2004, 2006, Post and Parkinson 2012). However, recent studies found that for particular species recreational catches can be comparable to commercial landings (Coleman et al. 2004, Zeller et al. 2008, Veiga et al. 2010). Consequently, it has been clearly established that recreational catches should be taken into account in fisheries management (Coleman et al. 2004, Lewin et al. 2006, Ihde et al. 2011).

1.2 Research gaps

Different challenges have been pointed out in relation to the management of coastal fisheries, including the heterogeneity among users, resource use patterns and the dynamics of coastal ecosystems supporting fisheries (Morales-Nin et al. 2010). EAF has also been considered in recreational fisheries (Arlinghaus and Cowx 2008). One of the main challenges to address for its success is to account for the dynamics resulting from angler behaviour (Arlinghaus and Cowx 2008). In contrast to commercial fishermen who focus on optimizing economic gains, recreational anglers have a more complex suite of motivations (Hunt 2005, Johnston et al. 2010). In addition to catch-related factors (i.e., fishing quality), other attributes that maximize personal utility may include environmental quality or ease of access. Therefore, a better understanding of the processes governing angler site choice is required to provide insights into the spatial management of recreational fisheries.

One constrain to the implementation of EAF is our limitation in understanding how social-ecological systems operate (Berkes 2012). The complex nature of socio-ecological systems constitutes a major challenge to our capacity for predicting fishing behaviour (Tidd et al. 2012). In regard to the spatial dimension of such systems, spatial heterogeneity has only recently been considered in recreational fisheries science (Parnell et al. 2010), primarily in assessing overexploitation risk in freshwater ecosystems (Post et al. 2002, Post et al. 2008, Hunt et al. 2011). Although there is an increasing concern about the impacts of recreational fisheries and the need to assess its spatial distribution, few assessment plans incorporate this activity. The spatial distribution of fishing effort is often considered homogeneous (Morales-Nin et al. 2010). The spatial dimension of fisheries is frequently ignored because it usually demands sophisticated social-ecological approaches and technology suited to obtaining fine-scale position data of both fish and anglers (Hunt et al. 2011, Fenichel et al. 2012, Post and Parkinson 2012). One reason can be attributed to the scarcity of reliable data and efficient monitoring programs (Post et al. 2002, Arlinghaus 2006b). Another constraint is the limited availability of analytical methods to dealing with partial data, complex interactions and non-linearities. Recent works in this field promise new opportunities for incorporating such complexity into EAF (Soykan et al. 2014).

Beside the need for considering human factors, a better understanding of the EFH and abiotic factors is required to assess fishery resources. EFH analysis relies on sampling methods and remote sensing techniques, together with spatial analysis methods, to identify suitable habitat for fish species (Valavanis et al. 2008). Benthic habitat mapping has an important role in the characterization of EFH of demersal species, however our knowledge of the spatial structure of marine ecosystems is still scarce due to our limited capacity for observing marine habitats. The development of new monitoring tools and methods is therefore required to advance in the identification of EFH. Furthermore, knowledge of fish movement is still lacking, especially for species that are mainly targeted by recreational fisheries. The recent advent of

acoustic telemetry systems and the development of miniature tags offer new opportunities for examining the movements of small-bodied species in nearshore ecosystems.

Finally, there is also the need for better management tools (Borja 2014). Identification of science and policy tools is a relevant factor for our capacity to implement EAF (Essington and Punt 2011). Advanced methods are needed for dealing with complex issues in marine data like SA, zero-inflated distributions or non-linear effects; whereas the incorporation of uncertainty measures in the models supposes a key challenge (Foley et al. 2010). Hence, there is a need for operational tools to put in practise scientific principles and thus support the effective implementation of EAF (Arkema et al. 2006).

1.3 Objectives

The goal of this thesis is to propose a general framework for assessing the spatial dimension of the coastal recreational fisheries using quantitative methods and computational tools. The aim is to advance in our understanding of angler spatial behaviour using a holistic approach based on empirical data and statistical models. The proposed approach relies on the recent development of monitoring methods and marine technologies, the availability of new environmental datasets and the advent of ecoinformatics (Michener and Jones 2012), especially within the fields of species distribution models (SDM, see Box 1.1) and geographic information system (GIS) methods. The integration of spatial-explicit information on human, biotic and abiotic components of the socio-ecological system is intended to serve the basis of decision making systems to support EAF.

Specifically, the aims of this thesis are:

- Develop a drop-camera system for monitoring benthic habitats
- Assess the spatial distribution of essential fish habitats, specifically seagrass meadows, in relation to biophysical parameters.
- Quantify the movements of the main fish species targeted by the recreational fishery
- Assess the spatio-temporal distribution of the fishing quality
- Model angler behaviour for predicting fishing effort and fishing harvest, while considering biotic, abiotic and human factors.

In order to test the proposed framework, one of the most popular coastal recreational fisheries in the Mediterranean Sea is used as case study in Palma Bay (Mallorca Island, Spain). The selected fishery, locally known as 'roquer', is practised from boats using hook-and-line, takes place over seagrass and rocky habitats, and captures a wide range of small-bodied species (Lloret et al. 2008, Alós and Arlinghaus 2013, Seytre et al. 2013). Recreational fisheries in Mallorca are open-access and managed through fishing licenses, conservation measures and spatial access (Morales-Nin et al. 2010). In the 'roquer' fishery, fish consumption is one of the main motivations (Cardona and Morales-Nin 2013) and concentrates most of the recreational fishing effort (Morales-Nin et al. 2005). This is a mixed-species fishery that targets on small-bodied species (eg. *Serranus scriba*, *Diplodus annularis*, *Coris julis*) and has received major attention in previous studies (e.g., Morales-Nin et al. 2005, Cardona et al. 2007, Lloret and Riera 2008, Alós and Arlinghaus 2013). Enforced regulations include bag limits (5 kg per day and fisher of any fish species),

gear limits (two rods with maximum of 3 hooks each), closed seasons and minimum legal size limits for some species. Spatial access is regulated through MPAs.

The selected study area, Palma Bay, corresponds to a marine temperate ecosystem dominated by seagrass. Palma Bay is a large (31 km wide), shallow (50 m maximum depth) bay located on the southern part of Mallorca Island, NW Mediterranean (Figure 1.2). Palma Bay is under ecological pressure from humans because the surrounding municipalities have 44.8% of the population of Mallorca and are the main targets for tourism in Balearic Islands. This coastal population and the high concentration of marinas contribute to this bay being as one of the most recreationally fished areas in Mallorca (Morales-Nin et al. 2005). The dominance of rocky habitats and the endemic seagrass *Posidonia oceanica* (Diaz Del Rio 1993) provide an adequate setting for the 'roquer' fishery.

Box 1.1 Species distribution models

Species distribution models (SDM) have been extensively used in conservation planning and management (Peterson et al. 2002). Note that in the context of this thesis, the nomenclature of SDM not only considers animal species but also includes humans (i.e., anglers). Such models relate species distribution data (e.g., presence-absence or count data) to environmental characteristics in order to improve our understanding of the effects of environment on species distribution (inference) and our ability to predict species distributions (Crase et al. 2012).

However, achieving these objectives has proved challenging. One of the most important drawbacks of species distribution data is spatial autocorrelation (SA; Legendre 1993), that is, observations are not only related to environmental conditions, but also to one another because of the geographic distance between them. SA may lead to (1) incorrect assessment of the ecological processes causing the observed distribution and (2) poor predictive capabilities.

A summary of the different SDM used in this thesis is presented in Table 1.1. Details on each one can be found in their respective Chapters.

Table 1.1 Comparison of species distribution models used in this thesis. GLMM, generalized linear mixed model; BRT, boosted regression trees.

Model name	Bayesian Kriging	Predictive process approach	GLMM	BRT
Inference	Bayesian	Bayesian	Frequentist	Machine-learning
Distribution	Bernouilli	Logistic	Gaussian	Hurdle
Type of response	Linear	Linear	Linear	Non-linear
R package	*spBayes*	*spBayes*	*lme4*	*dismo*
Observations	64	857	380-392	26823
Fit estimation	MCMC	MCMC	REML	Deviance
Response variable	Seagrass cover	Seagrass occurrence	Fishing quality	Boat counts
Predictor variables	3	6	7 fixed + 2 random	20
Interactions	No	No	Yes	Yes
Uncertainty	Credible Interval	Credible Interval	Bootstrap	Bootstrap
Chapter	2	3	6	7

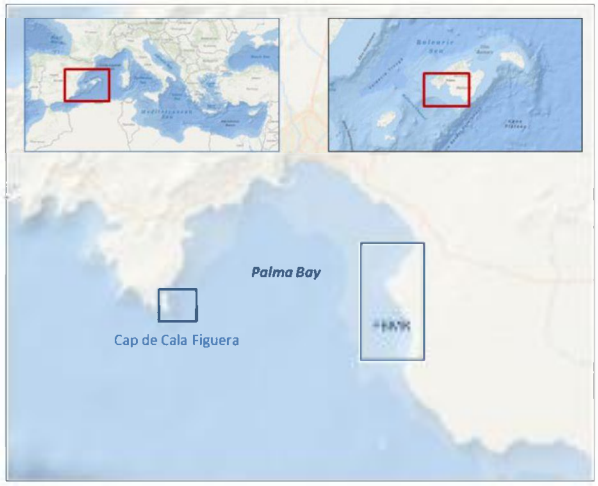


Figure 1.2 Palma Bay

Conservation measures in Palma Bay include two marine protected areas (Figure 1.2), which were declared to protect the seagrass meadows from human pressures. The first one is a marine area called "Cap de Cala Figuera", located in the western area of Palma Bay. It was declared as a Site of Community Importance (SCI, Natura 2000) in 2006, but specific management regulations for fisheries are not currently implemented. The second area, Palma Bay Marine Reserve (PBMR), is a MPA located in the eastern part of Palma Bay. PBMR protects an open water area that extends from the shoreline to the 30 m isobath. It was created in 1982, but human activities were not regulated in the reserve until 1999. Since 1990, several artificial reefs have been deployed to dissuade illegal trawling in the area. This MPA is zoned into two management areas of differing levels of protection: (1) an Integral Zone (≈2 km^2), where all fishing activities are prohibited; and (2) a Buffer Zone (≈24 km^2), where artisanal fishing is allowed under certain restrictions (eg. limited access, gear restrictions) and recreational fishing is banned 3 workdays a week, a minimum hook size (7 mm gape) is required, and fishing tournaments are banned.

1.4 Structure of the thesis

The conceptual model of this thesis, together with different transversal issues, is presented in Figure 1.3. In addition, a summary of the fieldwork activities carried out during the thesis is provided in Box 1.2. First, EFH were identified through the use of monitoring tools and environmental models (**Section II**). Benthic habitat mapping received major attention, since the 'roquer' fishery targets on demersal fish species associated to seagrass meadows and rocky bottoms. Previous maps on benthic habitats at Palma Bay only covered partial areas of the study area (Posidonia-LIFE map & Diaz Del Rio 1993). Therefore, a benthic mapping campaign was designed to monitor neashore ecosystems (i.e., up to 40 m depth) at Palma Bay. A low-cost, novel drop camera system was developed to acquire standized vertical geo-referenced images from seabottom (Chapter 2). However, our aim was not only mapping benthic habitats, but also estimating the effects of different biophysical variables (e.g. depth, wave exposure) on seagrass cover and occurrence. Accordingly, we implemented different hierarchical models for assessing such relationships and predicting seagrass cover (Chapter 2) and occurrence (Chapter 3) at unsampled locations.

In **Section III**, fish movement is examined with a two-fold objective. Firstly, to describe the extent of the home range size of the main target species, in order to define the spatial scale of further analysis (Chapter 6 and Chapter 7). Secondly, to evaluate whether this information could be used for MPA design and the assessment of potential spillover effects. Fish mobility was analysed combining new marine technologies (i.e., acoustic telemetry) and conventional methods (i.e., external tagging) at PBMR. Information

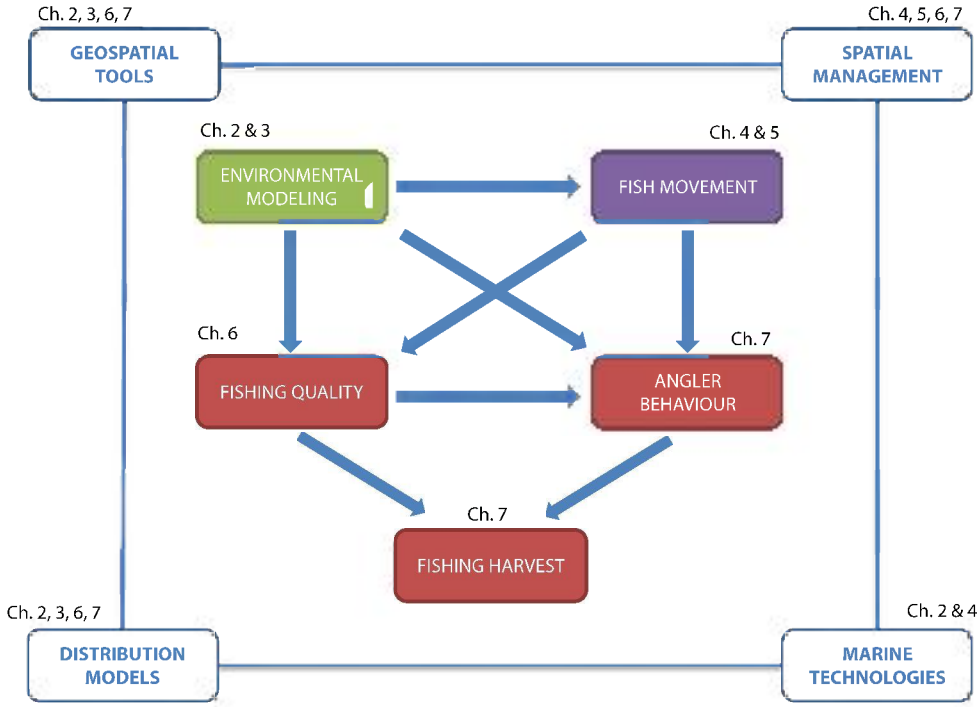


Figure 1.3 Conceptual model. Colored boxes represent the different components considered for assessing the spatial dimension of the recreational fishery. White boxes represent methods, tools and other transversal issues like spatial management (i.e., MPA) that have been integrate throughout this thesis. The number of Chapters (Ch.) where each component is mainly taken into account is indicated for each box.

on benthic habitats from the previous section (i.e., Posidonia-LIFE map, Chapter 2) was used for allocating acoustic receivers in areas dominated by seagrass meadows. Two important species were analysed in depth: the painted comber, *Serranus scriba* (Chapter 4); and the annular seabream, *Diplodus annularis* (Chapter 5). In addition, a summary of previous studies with other target species was generated for supporting the assessment of different fishing-catch metrics (Chapter 6).

Fishing-catch metrics, also referred as fishing quality, and the spatio-temporal patterns of boat anglers (i.e., fishing effort and harvest) are considered in more detail in **Section IV**. This section is focused on the human component of the fishery. A geospatial framework was provided for assessing and mapping the spatial distribution of different fishing quality metrics (Chapter 6). Such framework was based on experimental angling sessions and predictive modeling. This approach took into account the environmental information generated in Section II, and relied on the assumption that fish mobility is reduced (Chapter 4 and Chapter 5). Then, boat angler behaviour was analysed in order to predict angler site choice (Chapter 7). This approach used shipboard survey data together with previous information: environmental data (Chapter 3) and fishing quality (Chapter 6). Given the complexities of angler behaviour (e.g., interaction effects and non-linear responses), a flexible machine-learning method with high predictive power was implemented. In addition, the spatial scale of analysis (i.e., 1 x 1 km) was determined by taking into account previous fish mobility estimates. Finally, the last step in the conceptual model was the estimation of

fishing harvest (Chapter 7). Using the previous model of angler behaviour, quantitative estimates of fishing effort (i.e. boat outings) were predicted. The fishing effort calculations were then combined with the model of fishing quality (i.e., yield per unit effort) to provide estimates of total fishing harvest. Such an approach was carried out through numerical simulations and bootstrap methods which, in turn, allowed the quantification of uncertainty estimates.

Finally, **Section V** includes a general discussion and the main conclusions of the present thesis (Chapter 8).

Box 1.2 Summary of the main fieldwork methods

Different fieldwork activities that were carried out in this thesis are summarized:

Drop-camera: remote camera dropped from a boat and used for acquiring seabed images. This information was used for mapping benthic habitats. One study was carried out for estimating seagrass cover at PBMR (Chapter 2), whereas a second study focused on seagrass occurrence throughout the entire study area (Chapter 3).

Acoustic tracking: An acoustic telemetry network deployed at PBMR for tracking fish individuals tagged with acoustic transmitters. Used for tracking *Serranus scriba* (Chapter 4) and *Diplodus annularis* (Chapter 5).

Conventional tagging: Mark and recapture experiments using external T-tags carried out across the study area. Information on recaptures was used for assessing the movements of *Diplodus annularis* (Chapter 5).

Experimental angling: Angling sessions using a standardized protocol (e.g. gear type, fishing time, bait type). They were carried out between 2006-2007 on 49 locations for measuring different fishing quality metrics (Chapter 6).

Figure 1.4 Spatial allocation of fieldwork activities by Chapter.

Ship-board surveys: Conducted for geo-referencing angler boats during the period 2005-2010, with the exception of 2008. Angler boat positions were then used for estimating fishing effort and total harvest in Palma Bay (Chapter 7).

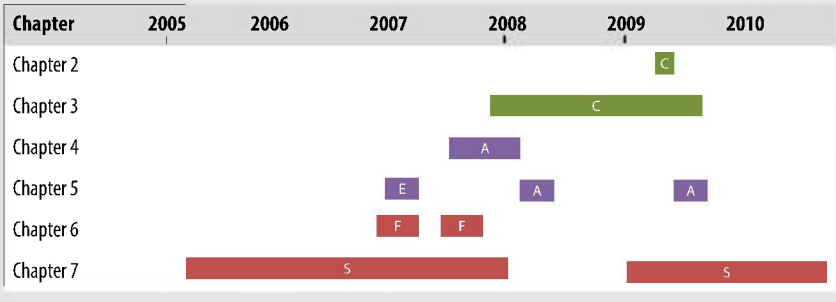


Figure 1.5 Calendar of field work activities by Chapter. Methods are represented by letters. C: drop-camera system; A: acoustic tracking; E: external tagging, F: experimental angling; S: ship-board surveys.

SECTION II. ENVIRONMENTAL MODELING

Chapter 2
Developing a drop-camera system for monitoring seagrass meadows

ABSTRACT:

A low-cost, novel drop camera system was designed and used to acquire standardized images that were used for estimating *P. oceanica* cover at PBMR. A simple, semi-quantitative cover index through visual inspection allowed robust estimates that are free of between-observer bias. A Bayesian kriging approach was implemented through a hierarchical model for non-Gaussian data. The map that was produced matches well with a previous map of the presence-absence of *P. oceanica* that was produced by combining side scan sonar and aerial photography. The influence of bathymetry, near-bottom orbital velocities (U_b) and slope on cover distribution were evaluated using a generalized linear model, while taking into account the spatial dependence between observations. We found that the important environmental variables were depth and U_b, while no effect of slope was found. The approach used here allowed us to not only map the cover of *P. oceanica* but also to provide spatial-explicit information of prediction uncertainty.

2.1 Introduction

Benthic habitat mapping plays an important role in the conservation and management of seagrass meadows, especially within the context of marine protected areas (MPAs; Jordan et al. 2005, Stevens and Connolly 2005, Grech and Coles). Underwater photography and videography have been demonstrated to be powerful tools for monitoring benthic communities, especially because they are non-destructive methods for species identification that can provide observations over large areas (Holmes et al. 2007). In addition, the development of small, remotely-deployed devices have overcome the main limitations of SCUBA divers and oceanographic vessels, allowing the monitoring of great expanses from small boats at low cost and high efficiency (Stevens and Connolly 2005).

Different statistical approaches have been used for modeling the spatial distribution of seagrasses and for examining their relationships with different environmental variables (Kelly et al. 2001, Fonseca et al. 2002, Fourqurean et al. 2003, Bekkby et al. 2008). Statistical analysis of these data is challenging because of the existence of spatial autocorrelation. Kriging is a family of geostatistical methods that explicitly incorporate the spatial structure of the data. Different types of kriging have previously been used to map seagrasses, such as indicator kriging (Holmes et al. 2007, Kendrick et al. 2008) and ordinary kriging (Fourqurean et al. 2001, Zupo et al. 2006, Leriche et al. 2011). However, as pointed out by Holmes et al. (2007), geostatistical models usually assume a Gaussian distribution. However, the type of data usually available for mapping seagrass meadows is presence-absence, or percent cover, which do not necessarily conform a Gaussian distribution. Recently, the implementation of Bayesian kriging has been demonstrated to be a useful tool to incorporate spatial effects that result from spatial autocorrelation, even when dealing with non-Gaussian distributions (Banerjee et al. 2004).

We combine seabed images and geostatistical analysis for extensive beds of *P. oceanica* (L.) off Mallorca. This species is endemic in the Mediterranean Sea, where it is the dominant and most abundant seagrass species and forms extensive meadows on both soft and hard bottoms from the sea level down to 40 m (Duarte 1991, Boudouresque et al. 2009). The current status of *P. oceanica* is especially critical because this long-lived species grows very slowly (Marbà and Duarte 1998) and is very sensitive to natural and anthropogenic disturbances (Boudouresque et al. 2009). The specific goals of this Chapter are 1) to present a standardized method for image acquisition from a drop camera that allows the estimation of seagrass cover using a semi-quantitative scale estimated by visual inspection; 2) to evaluate the effect of some key environmental variables on seagrass cover; 3) to generate a probabilistic map of seagrass cover that can be used as a proxy for the status of *P. oceanica* in a marine protected area (MPA) and 4) to incorporate uncertainty in the estimated maps of seagrass cover.

2.2 Materials and methods

2.2.1 Survey device and data collection

In this Chapter, we measured seagrass cover using a customized prototype of a non-invasive drop camera system (Subcam, Albatros Marine Technologies S.L.) (Figure 2.1). This system was used in a 5-m

length motorboat and consisted of a video camera (SONY 1/3" CCD, 3.6 mm lens, 1 lux / F 1.2) mounted on a metallic structure that allowed us to obtain vertical images at the same distance (148 cm) from the sea bottom. The area covered by the camera was 0.9 m^2. The camera was connected to an on-board computer via an umbilical cable (40 m length). Real-time images were visualized with custom software (Visualizer, Albatros Marine Technologies S.L.) that captured georeferenced images.

We examined the data of 112 sampling locations from between 5 and 35 m depth, collected between May 2009 and June 2009 at PBMR (Figure 2.2). During this season, *P. oceanica* reaches its maximum leaf length (Fourqurean et al. 2007), which facilitated the identification of *P. oceanica* in localities of low cover. At each location, three images were captured in succession at random sampling positions separated between 2 and 10 m apart. We selected days with gentle winds to minimize boat drift. In total, we recorded 336 images. Each of these 336 images was manually processed for determining the cover of *P. oceanica* by three independent trained observers (see subsection 2.5.1 for the assessment of the between-observer bias).

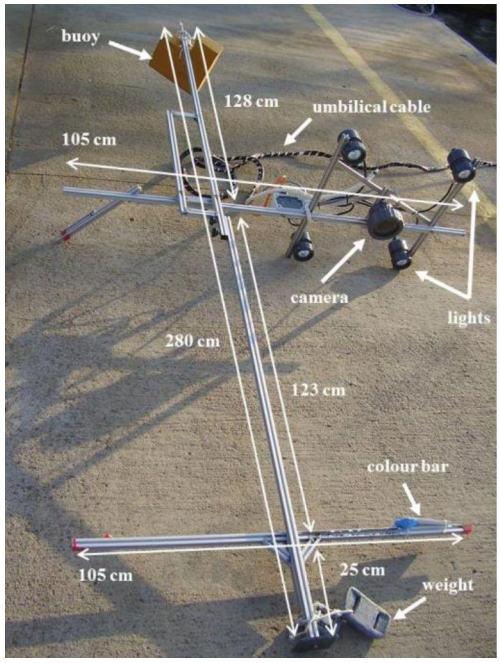


Figure 2.1 Subcam (Albatros Marine Technologies S.L.) system. A video camera is mounted on a metallic structure to obtain standardized images of seagrass cover. The system is dropped from a small boat by an umbilical cable that permits obtaining real-time images.

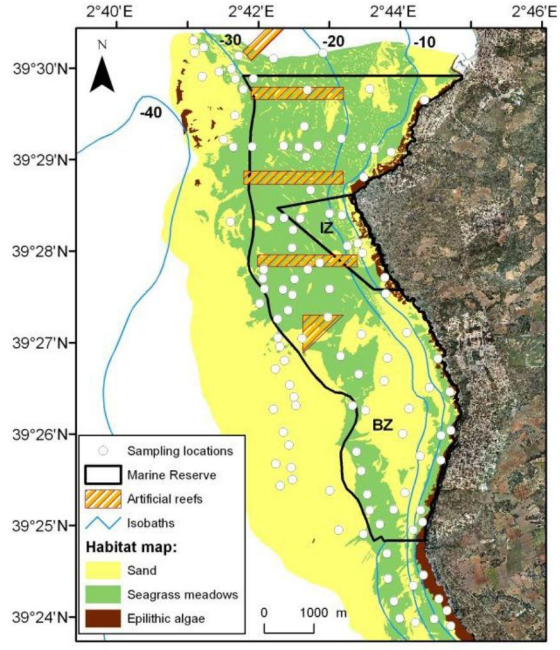


Figure 2.2 Map of the study area showing the sampled locations. Palma Bay Marine Reserve (PBMR) boundaries enclose the Integral Zone (IZ) and the Buffer Zone (BZ). The location of the zones of artificial reefs in PBMR are presented.

2.2.2 Quantification of seagrass cover

Image classification was based on the Braun-Blanquet Cover Abundance (BBCA) scale, previously used for seagrass research (Fourqurean et al. 2001, 2003, Madden et al. 2009). The BBCA assesses cover

according to a scale that has 25% intervals with an additional low cover class up to 5% (Table 2.1). Sample images with BBCA scores can be found in Appendix A. We then transformed the BBCA scores to the Average Covering Index (ACI), which assumes that each discrete value corresponds to the mean point of each class interval (Boudouresque 1971, van der Maarel 1979).

Table 2.1 Braun-Blanquet Cover Abundance (BBCA) scale and Average Covering Index (ACI). Each habitat type was scored in each image according to this scale.

BBCA scale	Interpretation	ACI (%)
0	Absence	0
1	< 5% cover	2.%
2	5-25% cover	15
3	25-50% cover	37.5
4	50-75% cover	62.5
5	75-100% cover	87.5

The statistical unit for the foregoing analysis was the location. Therefore, first the three ACI scores of an image (one per observer) were averaged. Then, the averaged ACI scores of the three images from the same location were averaged again, to obtain a single ACI value per location.

2.2.3 Predictor variables

Three key environmental variables were selected a priori as putative explanatory variables of seagrass cover. We generated models for bathymetry, slope and near-bottom orbital velocities in the domain vegetated by *P. oceanica,* as determined by a previous map of benthic communities (*Posidonia*-LIFE map, Government of Balearic Islands, http://lifeposidonia.caib.es). A digital bathymetric model (15 x 15 m grid size) was created using original bathymetric contours provided every 1 m (Posidonia-LIFE map). We then computed the slope (in degrees) at the same resolution using the Spatial Analyst extension of ArcGIS 9.2 (ESRI).

Near-bottom orbital velocities (U_b) at the study area were calculated from wave conditions to quantify the wave exposition experienced by the seagrass meadow. As water waves propagate from deep to shallow water, they change their properties (wave length, wave height and direction), and therefore, deep water waves have to be propagated to shallow waters (area of interest) using a numerical model (Infantes et al. 2009, Álvarez-Ellacuria et al. 2010, Infantes et al. 2011). Significant wave height (H_s), peak period (T_p) and direction were obtained from the closest WANA node, located approximately 15 km from the study site at 50 m depth. The WANA node provides operationally wave data by the reanalysis of a third generation spectral WAM model. The analysis of the wave data for the WANA node for the period 1996 to 2010 shows that, at the study area, the most energetic waves are from the SW, with an average H_s of 0.7 m and T_p of 5.5 s. These conditions were propagated to the shore using a numerical model based on the mild slope parabolic approximation (Kirby and Dalrymple 1983). The model output provided a wave field for the whole grid and at an appropriate scale (15 x 15 m grid size). Near-bottom orbital velocities (U_b) at the experimental locations were obtained from the wave propagation model outputs using linear wave theory (see Infantes et al. 2009 for details). This model does not take into account viscous effects such as the attenuation due to the presence of vegetation, which could overestimate the values of the U_b where a

dense seagrass meadow is present (Infantes et al. 2012). An extension of this model at the entire Palma Bay can be found in Chapter 3.

2.2.4 Data analysis

2.2.4.1 Observer bias

To assess between-observer differences, a set of preliminary trial and training sessions was completed based on a subset of images as a reference scale. Three observers then scored the cover of *P. oceanica* in all of the images. The existence of between-observer differences for ACI values on the five types of seabed considered was tested using an ANOVA. The data were not normal even after applying conventional transformations. Thus, a Monte-Carlo randomization test was completed for testing the null hypothesis of no-differences between observers (observations were randomly shifted between observers but constrained within an image). The ANOVAs were performed using the R software (R Foundation: www.r-project.org) and the *Vegan* package.

2.2.4.2 Data validation

We assessed the correspondence of the presence-absence of seagrass of the sampled photographs with a previously produced map. The *Posidonia*-LIFE map was built up by integrating side scan sonar, aerial photography and SCUBA observations (Figure 2.2). We defined the seagrass presence at a location when the mean of the ACI values was equal to or higher than 0.5% (this requires having, in at least 2 out of 3 images, a BBCA score of 1). Before overlapping sampled locations with a polygonal map, we defined a buffer area of 15 m around each location, to consider the uncertainty associated with the GPS error. We used the kappa index of agreement (Cohen 1960) to assess the reliability between observed values (i.e., sampled images) and expected values (i.e., benthic map). The kappa index varies between -1 and 1, where 1 indicates perfect agreement, -1 perfect disagreement, and 0 random assignment.

2.2.4.3 Spatial model

We implemented a predictive spatial model for point-referenced data of seagrass cover on the vegetated area of the MPA. Data used for the analysis only contained those locations where *P. oceanica* was present (n = 64). The predictive spatial model consisted of a Bayesian hierarchical model, as is implemented in the *spBayes* package (Finley et al. 2007).

The steps involved in the process are the following (see Appendix B for more details): 1) specifying a logistic regression model to relate environmental variables with seagrass cover; 2) defining a spatial correlation function to incorporate the spatial dependence in the model; 3) assigning prior distributions to set the probability distribution that represents the uncertainty of the model parameters; 4) using Markov Chain Monte Carlo (MCMC) methods to fit the model; 5) cross-validating the model using the root mean square error (RMSE) with a randomly selected subset of 15% (n = 10 locations); and 6) sampling the posterior distribution to map the predicted values as well as the uncertainty of the predictions.

2.3 Results

2.3.1 Observer bias

After some training, there was no evidence of between-observed bias. An ANOVA demonstrated that between-observer differences were non-significant (F= 0.0092). The probability of obtaining this value when the null hypothesis (no differences between observers) is true is 0.53; this value is based on 1,000 random permutations. Observers were freely permuted within images but images were not permuted.

2.3.2 Agreement between methodologies

Posidonia oceanica was detected at locations deeper than 6 m (coinciding with the minimum sampled depth) and down to 33 m depth (maximum sampled depth was 35 m). Results from validation of seagrass presence-absence at sampled locations in relation to the *Posidonia*-LIFE map are presented in Table 2.2. In only one sample was *P. oceanica* not detected at a location where it was expected to appear, in accordance with the *Posidonia*-LIFE map. This sampled location was at 31.5 m depth, and the distance to the closest edge between seagrass and sandy bottoms was 85 m (based on the *Posidonia*-LIFE map). In contrast, we detected seagrass at 7 sampled locations where it was not expected to appear. Four of these 7 locations had very low seagrass cover (ACI < 2.5%) and were placed at great depth, close to the lower limit. They were located near seagrass patches (at distances ranging between 17 and 110 m from the closest seagrass patch). The remaining 3 of the 7 locations had high seagrass cover (ACI = 87.5%) and corresponded in the *Posidonia*-LIFE map to *epilithic algae*. They were also located near seagrass patches (at distances ranging between 25 and 133 m from the closest seagrass patch), close to the upper limit. The kappa index based on Table 2 data was 0.86, which can be considered as very good (Landis and Koch 1977).

Table 2.2 Comparison between seagrass presence-absence at sampled locations and Posidonia-LIFE map

Sampling	Posidonia-LIFE map		Total
	Posidonia presence	Posidonia absence	
Posidonia presence	57	7	64
Posidonia absence	1	47	48
Total	58	54	112

2.3.3 Spatial distribution of seagrass cover

Maps of the covariates used for model prediction are presented in Figure 2.3. The depth ranged between 5.7 and 37.6 m, with a mean value of 24.4 m, while the slope ranged between 0 and 3.7°, with a mean value of 0.6°. The U_b ranged between 0 and 0.8 ms^{-1}, with a mean value of 0.07 ms^{-1}.

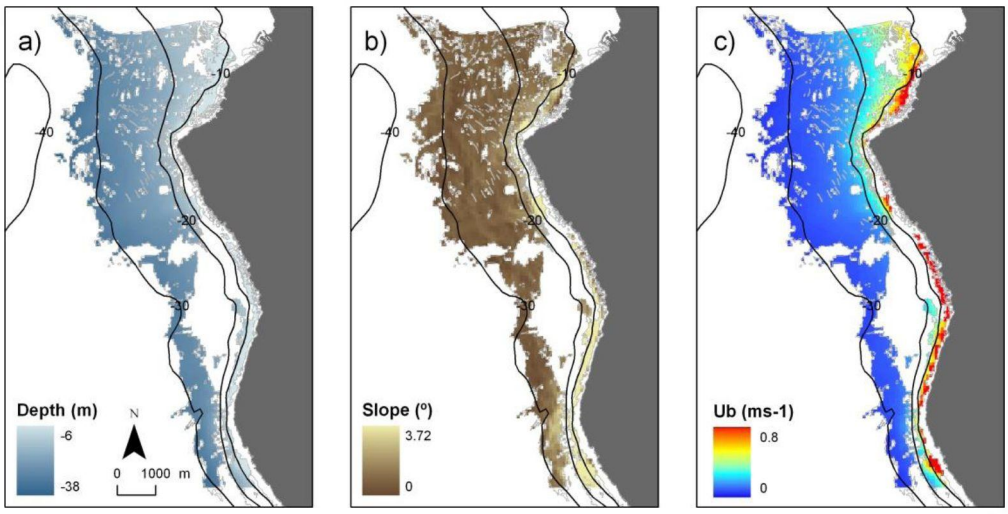


Figure 2.3 Environmental covariates on vegetated areas (gridsize 15 x 15 m). a) bathymetry; b) slope; c) near-bottom orbital velocities (U_b).

Parameter estimates of the spatial model are detailed in Table 2.3. Results suggested that depth contribution to the model is relevant because 95% CI not included zero, whereas the U_b is determinant at the 90% CI. *P. oceanica* cover would be negatively associated with depth and wave characteristics (Table 2.3). However, there was no relevant effect of slope on seagrass cover (Table 2.3). The median values of spatial parameters are 0.164 for σ^2, and 0.008 for ϕ (see the specification of the spatial effect variance -σ^2- and the spatial decay parameter -ϕ- in Appendix 1). The posterior mean of the effective range indicates a decline in the residual spatial autocorrelation at ≈350 m. The uncertainty of the latter parameter is relatively large (CI = 194 – 4207 m), which indicates that it cannot be estimated precisely.

Table 2.3 Parameter estimates of hierarchical model (posterior medians and upper and lower 2.5 percentiles). First block provide point and credible interval estimates of the intercept and covariates, indicating suggestive (*) and significant (**) coefficients. Second block provide estimates for the variance (σ^2), spatial decay (ϕ) and effective range parameters.

Parameter	Posterior median	0.025 Quantile	0.975 Quantile
Intercept**	9.203	1.590	18.614
Depth**	-0.303	-0.597	-0.063
NBOV*	-13.856	-32.119	2.630
Slope	-0.710	-2.190	0.758
σ^2	0.164	0.060	0.620
ϕ	0.008	0.001	0.015
Effective range (m)	367	194	4207

In the probability map (Figure 2.4a) the median value of each pixel's posterior distribution serves as prediction. The predicted probability of seagrass cover is mainly driven by depth. Note also that in some areas (i.e., in the SE zone) of shallow waters there is a decrease of seagrass cover, possible due to high U_b. The prediction error is presented by the range of 0.025 and 0.975 CI quantiles (Figure 2.4b). Cross-

validation performance of the spatial model (RMSE = 0.213) was similar to the model obtained by a non-spatial logistic model (RMSE = 0.214).

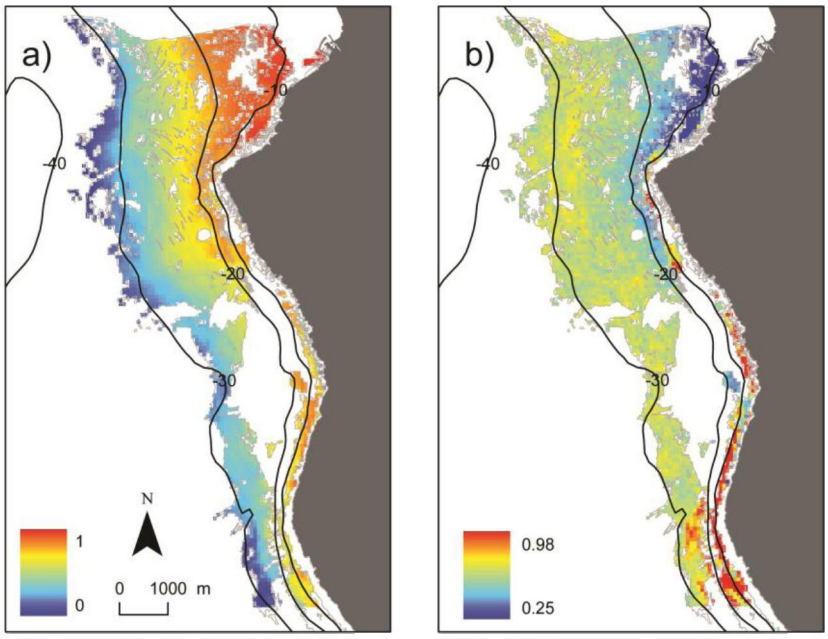


Figure 2.4 Spatial prediction of seagrass cover (gridsize 75 x 75 m): a) posterior estimates (median) for predicted seagrass cover; b) uncertainty of the prediction represented by the range between the lower and upper 95% posterior predicted intervals.

2.4 Discussion

Vertical photography from a drop camera permits coverage of a larger areas and collecting deeper samples than conventional vertical photography conducted by scuba divers. Other applications for seagrass mapping have used similar drop-cameras (Bekkby et al. 2008, Roelfsema et al. 2009) and tow-camera systems (Stevens and Connolly 2005, Holmes et al. 2007, Lefebvre et al. 2009). Holmes et al. (2007) stated that four main factors make image classification difficult: 1) camera angle; 2) proximity to plant; 3) conditions of light; and 4) water column turbidity. Our drop camera system successfully solved the first two factors, providing the same camera angle and distance to the seagrass for all of the images (Figure 2.5). Control over the conditions of lighting may be overcome with powerful lights and white balance correction, while water column turbidity constitutes an external factor that is more difficult to control. Nevertheless, these two factors are more relevant for species differentiation or automatic image classification and are not relevant for estimating seagrass cover in well identifiable seagrass meadows, as was our purpose. The estimation of seagrass cover was made by visual inspection and used a semi-quantitative scale that resulted in a rapid visual assessment technique. It is noticeable that, after some training with a small collection of reference images, no between-observer bias was detected.

The relationship of seagrass spatial distribution with bathymetry, wave exposure and slope has been explored in previous studies (e.g. Kelly et al. 2001, Krause-Jensen et al. 2003, Zupo et al. 2006, Bekkby et al. 2008, Infantes et al. 2009). In our study, depth and wave exposure (as U_b) were relevant, whereas slope had no effect on the seagrass cover. Depth was the most important factor that determined the spatial distribution of *P. oceanica* cover in our study area. This result is consistent with previous studies (Marbà et al. 2002, Zupo et al. 2006). However, in terms of its effects on seagrass cover, instead of a direct explanatory variable, depth should be considered as a proxy for light attenuation (Duarte 1991, Dalla Via et al. 1998, Duarte et al. 2007). The lower depth limit found in our dataset of 33 m conforms with other sources on *P. oceanica* (Marbà et al. 2002, Zupo et al. 2006, Duarte et al. 2007).

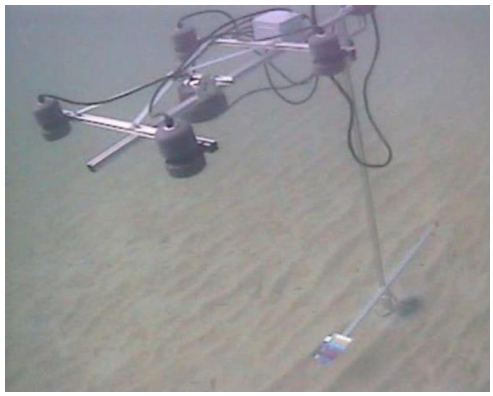


Figure 2.5 The camera system allowed to obtain images from the seabed with same camera angle and distance to the bottom

The negative relationship of seagrass cover with wave exposition (decreasing cover with increasing wave exposition) has been also demonstrated in previous studies (Kelly et al. 2001, Fonseca et al. 2002, Krause-Jensen et al. 2003, Bekkby et al. 2008). However, hydrodynamic conditions have been shown to have little influence on the meadow cover below the depth where wave action on the seafloor becomes negligible (Vacchi et al. 2010). In our study, we found a negative relationship between seagrass cover and U_b, as seagrass cover decreases with increasing near-bottom orbital velocities.

Slope has been identified as an important factor for the distribution of macrophytes (Duarte and Kalff 1990, Narumalani et al. 1997, Bekkby et al. 2008). Plant biomass decreases with increasing slope, as steep slopes will limit the rooting capabilities of aquatic plants. However, no effect of slope have been found in many study areas with small slope variations in gentle terrains (Krause-Jensen et al. 2003). Our study area was similar to the latter case, which would explain the lack of significance of slope in our model.

Uncertainty maps can be used to detect regions where the number of observations should be increased. Our results suggest higher uncertainty near the upper limit of *P. oceanica*. This pattern could be due to the effect of waves in shallow waters. This effect could probably be better modeled if more locations in shallow waters were measured. In deeper water, the uncertainty increased too, probably due to the vicinity to the lower-limit, where density is reduced and beds become patchy.

Spatial dependence of the cover has been reported for other *Posidonia* species (Holmes et al. 2007, Kendrick et al. 2008). Holmes et al. (2007) determined spatial dependence for *P. sinuosa* and *P. coriacea* over more than 2500 m. Similarly, Kendrick et al. (2008) determined ranges over 610 m up to *ca.* 3 km. In our study, the extent of spatial dependence (effective range) is close to 350 m. However, this parameter has been estimated with low precision and it could reach up to *ca.* 4 km (upper 95% CI). Pairs of locations at <350 m represent 1.5 % of this study, while those located at <4000 m represent 54.2 %. The low number of pairs separated at <350 m would suggest a low effect of spatial autocorrelation on parameter estima-

tion. This observation would explain the small difference in RMSE between the geostatistical model and the non-spatial model, and it suggests considerable homogeneity in bed cover.

Acknowledgements

This work would not have been possible without the help and support of the people that collaborated in the fieldwork, particularly M. Linde, I. Álvarez, S. Pérez, E. García, and J. Pericás. We thank Andrew Finley for support on spBayes. We also thank the support given by Albatros Marine Technologies SL, and Skua Gabinet d'Estudis Ambientals SLP. The habitat map was obtained from the Posidonia-LIFE program, Government of the Balearic Islands. This study was financed by the projects ROQUER (CTM2005-00283) and CONFLICT (CGL2008-958), which were funded by the Spanish Ministry of Research and Science.

Chapter 3
A Bayesian spatial approach for predicting seagrass occurrence

ABSTRACT:

In this Chapter we implement a Bayesian spatial approach to predict and map the probability of occurrence of seagrass *P oceanica* over a large area (≈100 km^2) at high spatial resolution based on environmental variables. We found that depth, near-bottom orbital velocities and a spectral pattern of Landsat imagery were relevant environmental variables, though we found no effect of slope or water residence time. We generated a data inventory of *P. oceanica* samples at Palma Bay, from three main sources: side scan sonar, aerial imagery and a customized drop-camera system (Chapter 2). A hierarchical Bayesian spatial model for non-Gaussian data was used to relate presence-absence data of *P. oceanica* with environmental variables in the presence of spatial autocorrelation (SA). A spatial dimension reduction method, the *predictive process approach*, was implemented to overcome computational constraints for moderately large datasets. Our results suggest that incorporating spatial random effects removes SA from the residuals and improves model fit compared to non-spatial regression models. The main products of this work were probability and uncertainty model maps, which could benefit seagrass management and the assessment of the ecological status of seagrass meadows. Moreover, benthic habitats could be used for identification of the essential fish habitats (EFH) of littoral fish species targeted by recreational fisheries.

3.1 Introduction

Seagrass meadows provide important ecosystem services including carbon sequestration, nutrient cycling, protection from erosion, and enhanced biodiversity (Hemminga and Duarte 2000). In the Mediterranean Sea, the dominant seagrass species is the endemic *P. oceanica* (L.) Delile, which forms extensive meadows on both soft and hard bottoms, from sea level down to 40 m (Duarte 1991, Boudouresque et al. 2009). *P. oceanica* is a long-lived marine clonal angiosperm characterized by very slow growing rhizomes (Marbà and Duarte 1998) and is sensitive to natural and anthropogenic disturbances (Boudouresque et al. 2009, Grech et al. 2012, Jordà et al. 2012b). Monitoring seagrass is particularly important because the European Water Framework Directive (Foden and Brazier 2007, López y Royo et al. 2009, Montefalcone 2009) and the Marine Strategy Framework Directive use seagrass as an indicator of ecosystem health and disturbance (Marbà et al. 2013).

Because of the biology of *P. oceanica* (i.e., clonal reproduction and low growth rate), SA may be high. In spite of the fact that SA is usually ignored, spatial models are a useful tool for relating seagrass presence with environmental variables and human threats (Fourqurean et al. 2003, Bekkby et al. 2008, Leriche et al. 2011). Bayesian hierarchical models have were applied in seagrass research (Chapter 2). However, it is not feasible to fit large datasets with such models using Markov chain Monte Carlo methods (MCMC) as it results in a problem known as the "big-n problem". This consideration is important when working with large areas and a large number of sampling locations. One solution is the proposed *predictive process approach* (Banerjee et al. 2008, Banerjee and Fuentes 2012). The *predictive process approach* allows a balance between model richness and computational feasibility, and it has been successfully employed in previous studies (Finley et al. 2009, Latimer et al. 2009, Eidsvik et al. 2012).

In this Chapter we implement a *predictive process approach* to analyze the spatial distribution of seagrass occurrence from point-based data and a set of environmental variables. This modeling approach allows testing the effects of environmental variables on seagrass occurrence while taking SA into account, and generates maps of probability of occurrence and its uncertainty. Moreover, spatial distribution of seagrass can be used for identifying essential fish habitats which, in turn, would be used for assessing the fishing quality (Chapter 6) and fishing effort (Chapter 7) across heterogeneous seascapes. We demonstrate such approach using data of *P. oceanica* at Palma Bay to assess and map its spatial distribution.

3.2 Materials and methods

3.2.1 Data collection

Within a study area of ≈100 km^2 (Figure 3.1), we determined the presence-absence of *P. oceanica* at Palma Bay using three different methods through a random sampling design (mean distance to the nearest neighbor location was 247 m, n = 857 locations). First, we used aerial photography imagery (Instituto Geográfico Nacional) to determine seagrass absence in shallow waters (n = 19 locations). Second, we used a recent survey conducted at PBMR by side scan sonar (Government of Balearic Islands, http://lifeposidonia.caib.es) to determine the presence-absence of seagrass in PBMR (n = 153 locations).

Finally, we used the underwater drop-camera system presented in Chapter 2 to collect standardized vertical geo-referenced images at 685 locations during expeditions between January 2008 and June 2009. At each location, three images were captured at random sampling positions separated by 2 to10 m. Image classification was based on the Braun-Blanquet Cover Abundance (BBCA) following the same methodology presented in Chapter 2**¡Error! No se encuentra el origen de la referencia.**. We defined the presence of seagrass at a location when at least 2 out of 3 images had a BBCA score equal to or higher than 1 (see Table 2.1).

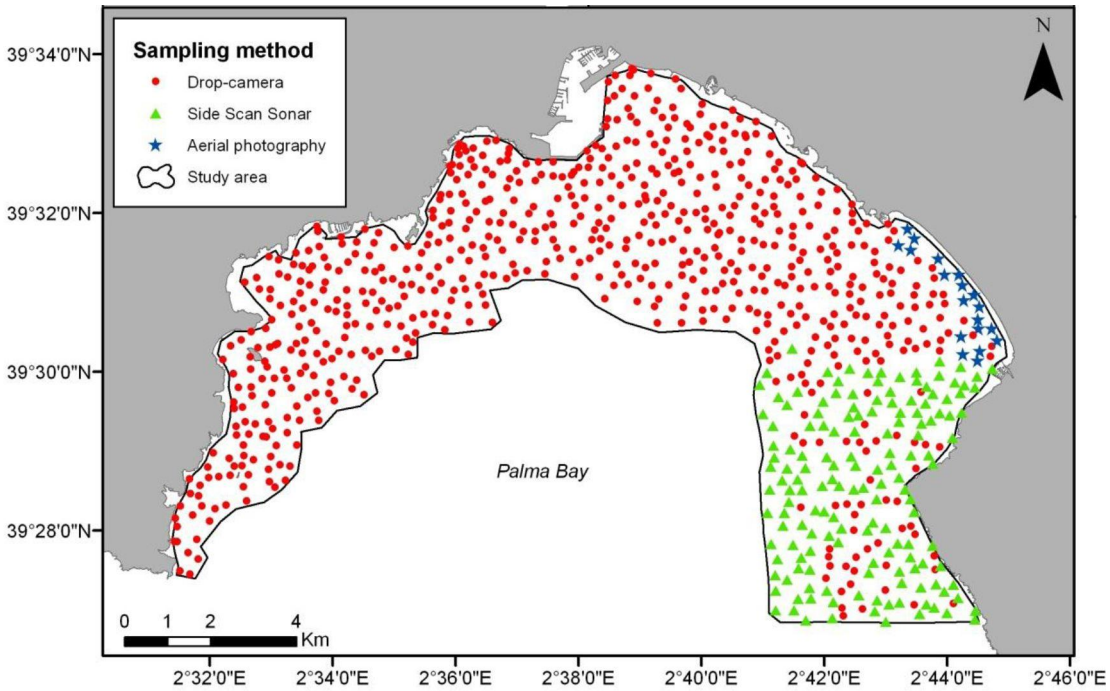


Figure 3.1 Palma Bay. Sampling locations classified by observation method: aerial photography, side scan sonar and drop camera.

3.2.2 Environmental variables

We generated models of environmental variables that were selected a priori as putative explanatory variables of *P. oceanica*. Those environmental variables included geomorphological (depth and slope), oceanographic (near bottom orbital velocity and water residence time), and multispectral data from Landsat bands. All variables were modeled in the study area using a regular grid of 50 x 50 m at Palma Bay.

3.2.2.1 Geomorphological variables

We used point-data sounding from digitized nautical charts (Instituto Hidrográfico de la Marina, 1:25,000) to generate a digital bathymetric model (DBM) using Multilevel B-spline Approximation (MBA) algorithm (Lee et al. 1997). Then we calculated the slope (SLP), measured in degrees, using a 3 x 3

neighborhood around each cell in the DBM. We used R v.2.9.1 (*MBA* and *spgrass6* packages) for the analysis.

3.2.2.2 Oceanographic variables

We quantified exposure to waves in the seagrass meadow by calculating near-bottom orbital velocities (U_b) in the study area from wave conditions (Infantes et al. 2009, Infantes et al. 2011). The significant wave height (H_s), peak period (T_p) and direction were obtained from the closest WANA node, located approximately 15 km from the study site at a 50 m depth. The WANA node provides wave data from the reanalysis of a third generation spectral WAM model site (see Infantes et al. 2009 for details). Data from the WANA node for the period 1996 to 2010 shows that the most energetic waves in the study area are from the SW, with an average H_s of 0.7 m and T_p of 5.5 s. These conditions were propagated to the shore using a numerical model based on the mild slope parabolic approximation (Kirby and Dalrymple 1983).

Water residence time (WRT) was estimated with a high-resolution ocean circulation model that reproduces the dominant patterns of the observed circulation in the bay (Jordi et al. 2011). The trajectory of virtual lagrangian particles introduced in the model at each grid point was determined by interpolating the model currents to the particle position. The time lapsed for each particle to travel a distance greater than 5 km from its initial position was used as estimate of the residence time. A new set of particles was released each 12 hours during the model run (6 months, May-October 2009). The residence time used in this study was averaged for each set of particles and interpolated to the regular grid of 50 x 50 m.

3.2.2.3 Landsat Enhanced Thematic Mapper Plus (ETM+)

Multispectral data by the Landsat ETM+ instrument were obtained from the Earth Resources Observation and Science (EROS) Center (http://eros.usgs.gov/). There are eight multispectral bands with a spatial resolution of 30 m for the six reflective bands, 60 m for the thermal band, and 15 m for the panchromatic band. A total of 72 Landsat ETM+ images were acquired for the study area for the period 1999-2009. Free-of-clouds pixel values were measured at the sea surface for each band, and the images were converted to at-sensor spectral radiance using radiometric sensor calibration (Chander et al. 2009) and interpolated to a regular grid of 50 x 50 m using an optimal statistical interpolation with a cut-off length scale of 500 m. A principal components analysis (PCA) of averaged values was applied to reduce the number of bands into two principal components (PC1 and PC2), which were used as predictor variables. This approach preserves the original spectral patterns while reducing interband correlation in the satellite data (Koutsias et al. 2009).

3.2.3 Data analysis

We implemented a predictive spatial model for point-referenced data for of seagrass occurrence in Palma Bay. The spatial predictive model was a Bayesian hierarchical model based on a Chapter 2 and implemented in the *spBayes* package (Finley et al. 2007). Because this study included a large number of observations (n = 857 locations), which results in the "big-n problem", we used a *predictive process approach* (Finley et al. 2009, Latimer et al. 2009, Banerjee and Fuentes 2012, Eidsvik et al.). The steps involved in the analysis workflow were the following (see Appendix B for details): 1) specifying a logistic regression model to relate environmental variables with seagrass presence-absence; 2) defining a spatial

correlation function to incorporate spatial dependence in the model; 3) selecting a reduced number of representative locations (knots) to introduce a second stage in the model and improve the computation speed; 4) assigning prior distributions to set the probability distribution that represents the uncertainty of the model parameters; 5) using Markov Chain Monte Carlo (MCMC) methods to fit the model; 6) selecting the best model from a set of candidate models using the Deviance Information Criterion (DIC); 7) cross-validating the model using the area under curve (AUC) with a randomly selected subset of 15% (n = 129 locations) to assess the model accuracy and select a threshold probability (i.e., through an optimization method) to classify probabilities into presence or absence; and 8) sampling the posterior distribution to map the predicted values (i.e., the median) and also the associated levels of uncertainty (i.e.,, 95% credible intervals) at a resolution size of 150 x 150 m.

3.3 Results

3.3.1 Environmental covariates

Maps of the covariates used for model prediction are presented in Figure 3.2. The depth (DBM) ranged from 0.3 to 42.7 m (Figure 3.2A), with a mean value of 24 m. The east area of the bay was gently sloped in comparison with the west area, which had steep slopes and a maximum value of 4.97° (Figure 3.2B). In contrast, the east area presented higher values of U_b because of exposure to the predominant SW wave climate (Figure 3.2C). U_b values ranged from 0 to 1.62 m/s. The WRT model results ranged from 2 to 8.96 d, with higher values at the NE area of the bay (Figure 3.2D). For the Landsat bands, the first two Principal Components (PCs) from the analysis accounted for 98% of the total variance in the original data set. PC1 was more closely associated with bands 1-5 and 7-8, whereas PC2 was more influenced by band 6.

3.3.2 Spatial distribution of *Posidonia oceanica*

The presence-absence dataset for seagrass is presented in Figure 3.3A. *P. oceanica* was detected between 2 m and 33 m of depth (maximum sample depth was 42 m depth). Results of the model selection are detailed in Table 3.1. The model that incorporated all variables was selected because of its low DIC value (see Appendix B step 6 for details). Parameter estimates of the model are detailed in Table 3.2. The credible 95% intervals (CI) suggested that DBM, U_b and PC2 were relevant because they did not include zero. However, SLP, WRT and PC1 were not relevant in determining *P. oceanica* ocurrence. Concerning the spatial autocorrelation (SA), the median values of spatial parameters were 13.873 for σ^2, and 0.001 for ϕ (see the specification of the spatial effect variance -σ^2- and the spatial decay parameter -ϕ- in Appendix B). The posterior mean of the effective range indicated a decline in the residual spatial autocorrelation at ≈4,811 m. This suggests that any observation (presence-absence) would be affected by other observations within 4,811 m. Figure 3.4A shows how the fitted semivariogram of the residuals of a non-spatial GLM reached an asymptote close to 5,000 m, whereas in Figure 3.4B the semivariogram of the residuals of the hierarchical Bayesian model remained flat (i.e., spatial independence). This illustrates that the Bayesian approach explicitly accounted for spatial dependence.

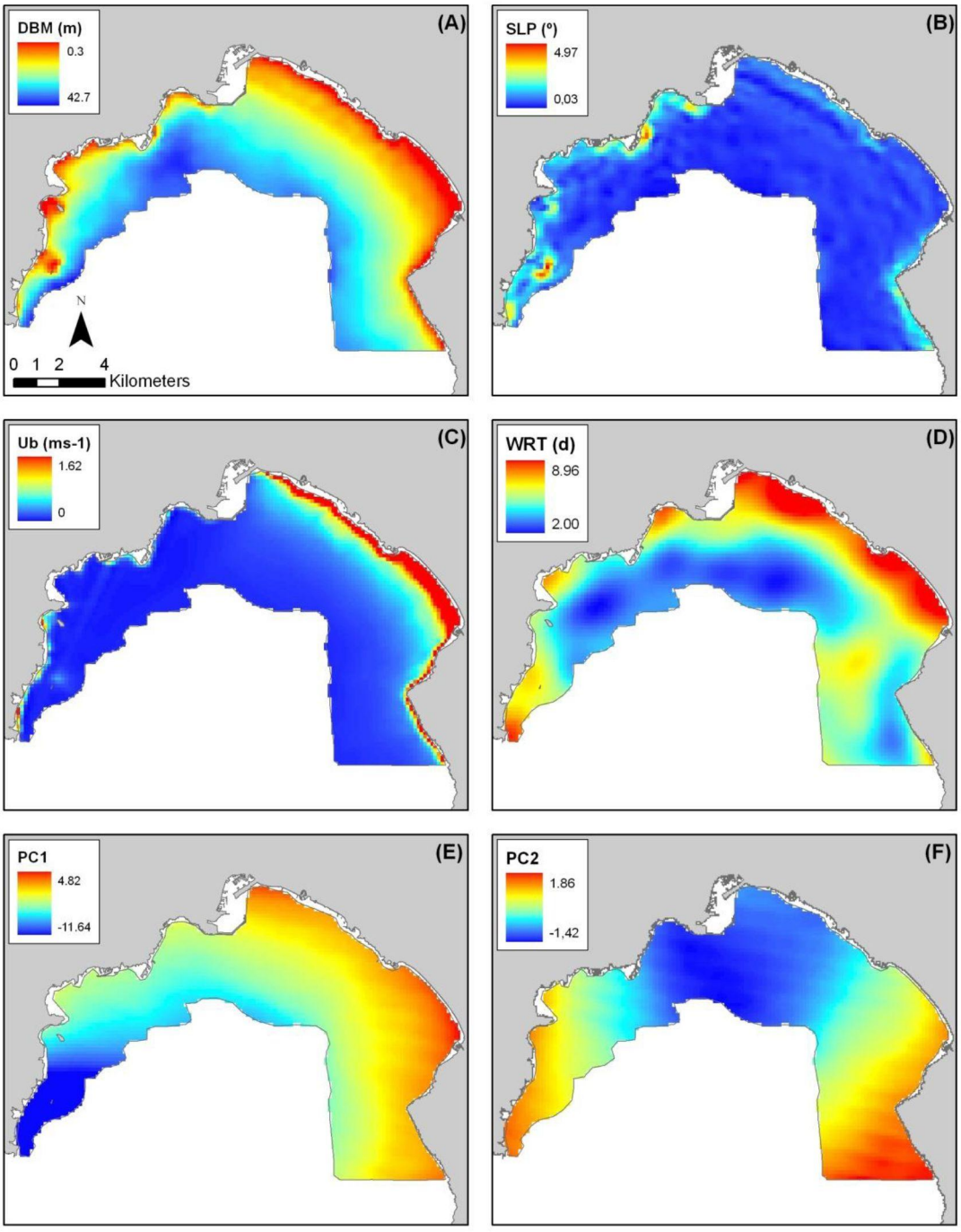


Figure 3.2 Environmental covariates (150 x 150 m grid): a) Depth (DBM), b) Slope (SLP), c) near-bottom orbital velocities (U_b), d) water residence time (WRT); e) Landsat PC1, f) Landsat PC2.

Table 3.1 Results of the model selection. Model selected (the one with lower DIC) is marked in bold.

Model	Environmental variables	DIC
1	DBM	922,67
2	SLP	970,61
3	WRT	970,61
4	U_b	972,84
5	PC1	975,54
6	PC2	926,97
7	DBM, PC2	896,96
8	DBM, WRT	917,09
9	DBM, SLP	930,41
10	DBM, U_b	812,90
11	DBM, PC1	926,29
12	DBM, U_b, PC2	746,97
13	DBM, U_b, WRT	794,96
14	DBM, U_b, PC1	792,69
15	DBM, U_b, SLP	795,06
16	DBM, U_b, PC2, PC1	766,56
17	DBM, U_b, PC2, WRT	762,53
18	DBM, U_b, PC2, SLP	758,83
19	DBM, U_b, PC2, SLP, PC1	750,38
20	DBM, U_b, PC2, SLP, WRT	757,01
21	**DBM, U_b, PC2, SLP, PC1, WRT**	**736,16**

Table 3.2 Parameter estimates of the selected model (posterior median and upper and lower 2.5 percentiles). The first block provides point and credible interval estimates of the intercept and covariates; the second block provides estimates for the variance (σ^2), spatial decay (ϕ), and effective range parameters.

Parameter	Posterior median	0.025 Quantile	0.975 Quantile
Intercept	11.981	6.700	19.888
DBM	-0.419	-0.601	-0.256
U_b	-9.756	-13.806	-6.411
PC2	1.228	0.031	2.773
SLP	-0.844	-1.953	0.195
PC1	-0.301	-0.676	0.272
WRT	-0.383	-1.175	0.181
σ^2	13.873	5.054	24.915
ϕ	6.24×10^{-4}	3.25×10^{-4}	1.20×10^{-3}
Effective range (m)	4,811	2,503	9,224

The probability maps of seagrass cover and the associated error are presented in Figure 3.3B and Figure 3.3D, respectively. The median value of each pixel's posterior distribution serves as the prediction value. The prediction error is presented by the range of 0.025 and 0.975 CI quantiles (Figure 3.3C).

Cross-validation performance of the spatial model resulted in an AUC value of 0.90 ± 0.03 (± sd), indicating very good predictive power. Contours indicating the presence of seagrass using the estimated probability threshold of 0.585 are shown in Figure 3.3D. The estimated extent of seagrass based on this threshold in the study area was 47.6 km^2.

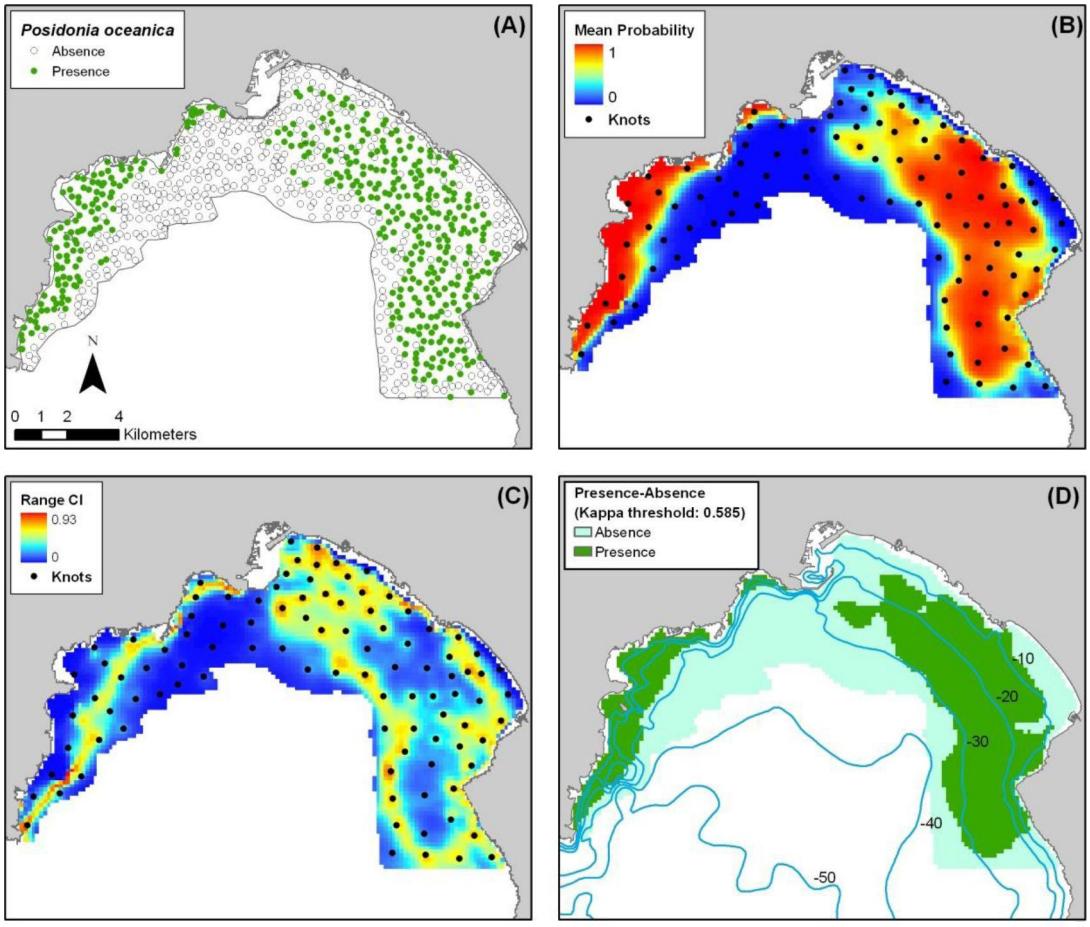


Figure 3.3 Spatial prediction of seagrass cover (150 x 150 m grid): a) observed values of presence-absence; b) posterior estimates (median) for predicted response surface Y(s) seagrass cover; c) uncertainty of the prediction represented by the range between the lower and upper 95% posterior predictive intervals, d) classification of presence-absence based on a threshold of 0.585.

3.4 Discussion

3.4.1 Distribution of *Posidonia oceanica* in Palma Bay

P. oceanica meadows dominate the seabed of Palma Bay at depths of up to 30 m. Meadows were found in two main patches (Figure 3.3D). In the eastern part of the bay, *P. oceanica* was also found in deeper waters, in a patch that occurred partially within the MPA of Palma Bay, where management efforts for seagrass began in 1982. On the other hand, two zones that were shallower than 30 m were not covered by *P. oceanica*. The first zone was the area close to Palma Beach, where there was high wave exposure and fine sands were the dominant component. The second zone was near the area of Palma harbour, where significant human pressures are present (e.g., coastal development, sewage, commercial boat anchoring). In this area, the scattered pattern of *P. oceanica* resulted in high uncertainty estimates.

3.4.2 Effect of environmental variables

Among the geomorphological variables, bathymetry had the greatest influence on *P. oceanica* distribution at Palma Bay. The relationship of seagrass ocurrence according to bathymetry can be explained by an irradiance gradient (Dalla Via et al. 1998, Duarte et al. 2007). The lower depth limit of 33 m in our dataset is consistent with the findings of previous studies (Marbà et al. 2002, Zupo et al. 2006, Duarte et al. 2007). On the other hand, the results indicated that slope did not have a relevant role in the spatial distribution of *P. oceanica*. Although slope has been identified as an important factor for the distribution of macrophytes (Duarte and Kalff 1990, Narumalani et al. 1997, Bekkby et al. 2008), there is sometimes no effect in cases with small slope variation in gentle terrains (Krause-Jensen et al. 2003), which may apply in our case.

A decrease of seagrass cover with increasing exposure to waves has been demonstrated in previous studies (Krause-Jensen et al. 2003, Bekkby et al. 2008, Infantes et al. 2009, Vacchi et al. 2010, Vacchi et al. 2012). In the present work, U_b was found to affect the distribution of seagrass, though the results from Chapter 2 found an unclear effect of U_b. In that previous study, the entire study area had the same orientation to wave exposure, which may not represent spatial variability. In fact, the present study found a difference in exposure between the eastern and western parts of the bay, highlighting the relevance of scale in interpreting the effects of environmental variables.

The other oceanographic parameter considered in this study, WRT, was not found to influence the distribution of the meadows at Palma Bay. WRT has been proposed as a good indicator to assess the vulnerability of the ecosystem to pollutants, and proved to have a definite effect on *P. oceanica* in a previous study (Orfila et al. 2005). However, it should be noted that the correlation between areas free of seagrass and WRT was found at values larger than 15 d, whereas the maximum WRT in our study area was only 9 d.

Landsat imagery has been used in previous studies as a direct source of presence-absence data for seagrasses in shallow waters (Roelfsema et al. 2009). Although no empirical data were available to calibrate the Landsat imagery and correlate it with turbidity or SST, we used principal components as a proxy. Bands 1 to 3, which have been related with water turbidity and chlorophylls (Erkkila and Kalliola 2004), were related to PC1. On the other hand, band 6, which has been correlated with SST (Thomas et al. 2002), was related to PC2. This second component seems to present some correlation with the spatial distribution of *P. oceanica* at Palma Bay (Table 3.2). Looking at Figure 3.2F, we can see how PC2 presents a gradient from the northern-center part of the Bay to the east and west.

3.4.3 Notes on the modeling approach

The purpose of this work was not only to map *P. oceanica* at Palma Bay, but also to evaluate the effect of different environmental variables in the presence of spatial autocorrelation. We have demonstrated that the modeling framework adopted in this work was able to remove spatial autocorrelation from the model residuals by incorporating a spatial error term (Figure 3.4). The flexibility of our modeling approach allowed the inclusion of other environmental variables that, if available, could enhance the richness and predictive power of the model.

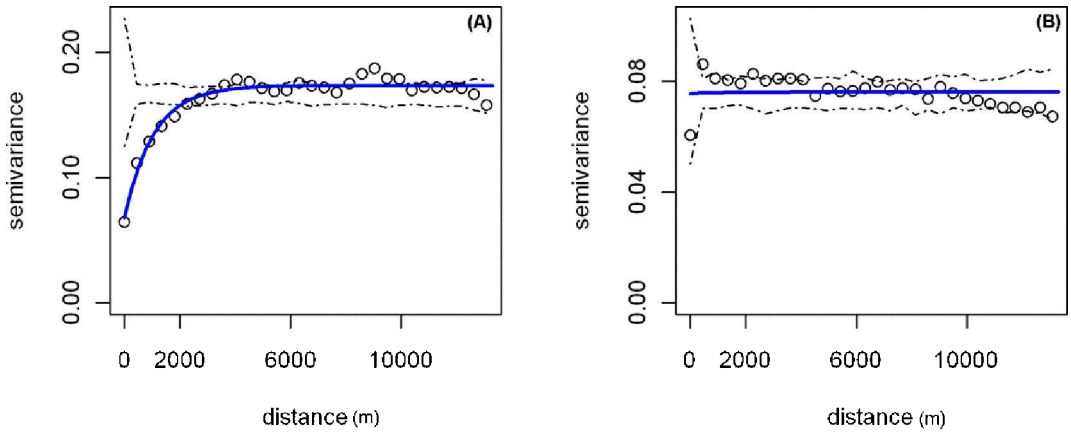


Figure 3.4 Empirical semivariograms computed for the residuals from a non-spatial GLM (a) and the residuals from the hierarchical model (b). Dashed lines represent envelopes of 99 permutations.

Uncertainty maps provide an important complement to any map of predicted presence-absence probability. This information could be used to identify areas where environmental variables cannot explain the distribution of the species. We found greater uncertainty close to edges of the meadow and in areas with scattered presence of seagrass. In addition, this information could be used to identify possible local human-related pressures, or other environmental variables that are not currently considered. Because extensive cartographies are now becoming available (eg. EUSeamap), the "big N problem" may become a constraint in modeling of species distribution. The *predictive process approach* appears to be an effective method for overcoming such problem that could be applied in other systems and has a great potential for being implemented in conservation planning and management.

Segrass meadows provide an adequate setting for the recreational fishery analysed in this thesis. Further works will use the information generated here to identify essential fish habitats (EFH). Together with sandy and rocky habitats, benthic habitats maps are used for assessing the spatial distribution of fishing quality (Chapter 6) and fishing effort (Chapter 7).

Acknowledgements

This work would not have been possible without the help and support of the people that collaborated in the fieldwork, particularly M. Linde, I. Álvarez, S. Pérez, E. García, and J. Pericás. We also thank the support given by Albatros Marine Technologies SL, and Skua Gabinet d'Estudis Ambientals SLP. This study was financed by the projects ROQUER (CTM2005-00283) and CONFLICT (CGL2008-958), which were funded by the Spanish Ministry of Research and Science.

SECTION III. FISH MOVEMENT

Chapter 4
Movement patterns of *Serranus scriba*

ABSTRACT:

In this Chapter, we examined the short-term movements of a small temperate fish, the painted comber *Serranus scriba* (Linnaeus 1758), within the marine protected area (MPA) of Palma Bay (NW Mediterranean), using passive acoustic telemetry. Fifteen adults were surgically implanted with acoustic transmitters and monitored between July 2007 and February 2008 for periods of up to 36 days. Inter-individual variability was detected for both spatial and temporal patterns. There were two principal movement behaviours that were recorded, with some individuals showing high site fidelity and others showing a more mobile behaviour moving out from the monitoring area. Observation-area curves indicated that a period between 3 and 5 days was required to determine home ranges of this sedentary fish. Home range sizes were small, and with a minimum shift of core areas occurring on a daily basis. Total minimum convex polygon areas (MCP) ranged from 0.102 and 0.671 km^2, whereas 95% kernel utilization distributions (KUD) ranged between 0.760 and 1.333 km^2. Core areas (50% KUD) ranged between 0.175 and 0.294 km^2. There were no significant differences in home range patterns between day and night periods. However, the use of the continuous wavelet transform (CWT) revealed diel rhythms on the detection pattern that could be related to a resting behaviour at night. Estimation of home ranges of *S. scriba* agrees with the sedentary habits of the Serranidae family, and suggests: 1) the potential use of MPAs for the sustainable development of the fishery of this small Serranid, and 2) its potential usefulness as bioindicator for assessing fine-scale patterns of fishing exploitation (Chapter 6 and Chapter 7).

4.1 Introduction

Acoustic telemetry has been used as an alternative as well as a complementary method to conventional mark and recapture studies for studying fish movements (Voegeli et al., 2001; Parsons and Egli, 2005; Abecasis et al., 2009). For example, this technology has allowed researchers to quantify the extent of fish home ranges within MPAs (e.g., Lowe et al., 2003; Parsons and Egli, 2005), determine site fidelity (e.g., Collins et al., 2007; Abecasis and Erzini, 2008) and obtain data on homing abilities (Kaunda-Arara and Rose, 2004; Jadot et al., 2006). In this technique, an acoustic transmitter is attached to an individual and the acoustic signal is received by a hydrophone. In addition, the recent development of miniature tags has allowed transmitters to be used on small fish, which has increased the size range of animals that can be tagged. The tracking process can be active (i.e., boat tracking with a directional hydrophone) or passive (i.e., deploying submersible omnidirectional receivers). From among the different systems available for acoustic telemetry, automated systems that use arrays of acoustic listening stations have become a popular research tool (Heupel et al., 2006). These passive systems can be designed to monitor various individuals' movements simultaneously in a broad range of spatial and temporal scales in order to infer spatial (e.g., home range) and temporal (e.g., diel activity) movement patterns.

The painted comber, *Serranus scriba* (Linnaeus 1758), is a littoral benthic fish that is distributed along the coasts of the Mediterranean and the Black Sea, as well as in the eastern Atlantic Ocean, from the Bay of Biscay to Mauritania (Bauchot 1987a). This species can be found from the intertidal zone to depths of 150 m, although it is more common at <20 m (Fasola et al. 1997), where it inhabits rocky bottoms and seagrass meadows (Guidetti 2000). *S. scriba* feeds on small fish and invertebrates such as crustaceans (Fasola et al. 1997) and is a simultaneous hermaphrodite (Fischer and Petersen 1987). This species is included in the FAO catalogue of species of interest to fisheries in the Eastern Central Atlantic and in the Mediterranean and the Black Sea (Tortonese 1986, Bauchot 1987a). *S. scriba* has been used as bioindicator of marine pollution (Roméo et al. 1999), and for monitoring temperate MPA effects (Francour 2000). In the Balearic Islands (NW Mediterranean), *S. scriba* is one of the most frequently targeted species for recreational boat anglers (Morales-Nin et al. 2005). Recent studies have used *S. scriba* to assess the impacts of recreational fisheries (Cardona et al. 2007, Alós 2008). Thus, information on movements of *S. scriba* is relevant for the management of recreational fisheries.

In this Chapter, we used acoustic telemetry to examine the short-term movement patterns of a small temperate fish, the painted comber, *S. scriba*. Specifically, the aims of the study were: (1) to quantify the home range and short-term movements of *S. scriba*; (2) to determine short-term residence; and (3) to determine the existence of diel patterns.

4.2 Materials and methods

4.2.1 Study site

The study was carried out between July 2007 and February 2008 at PBMR. Environmental parameters in the MPA were monitored using an oceanographic buoy from the Mediterranean Institute of Advanced

Studies (IMEDEA). The monitoring area in the present study was placed in the zone that encompasses both the Integral and Buffer zones, which is mainly dominated by seagrass meadows of *Posidonia oceanica* (Figure 4.1).

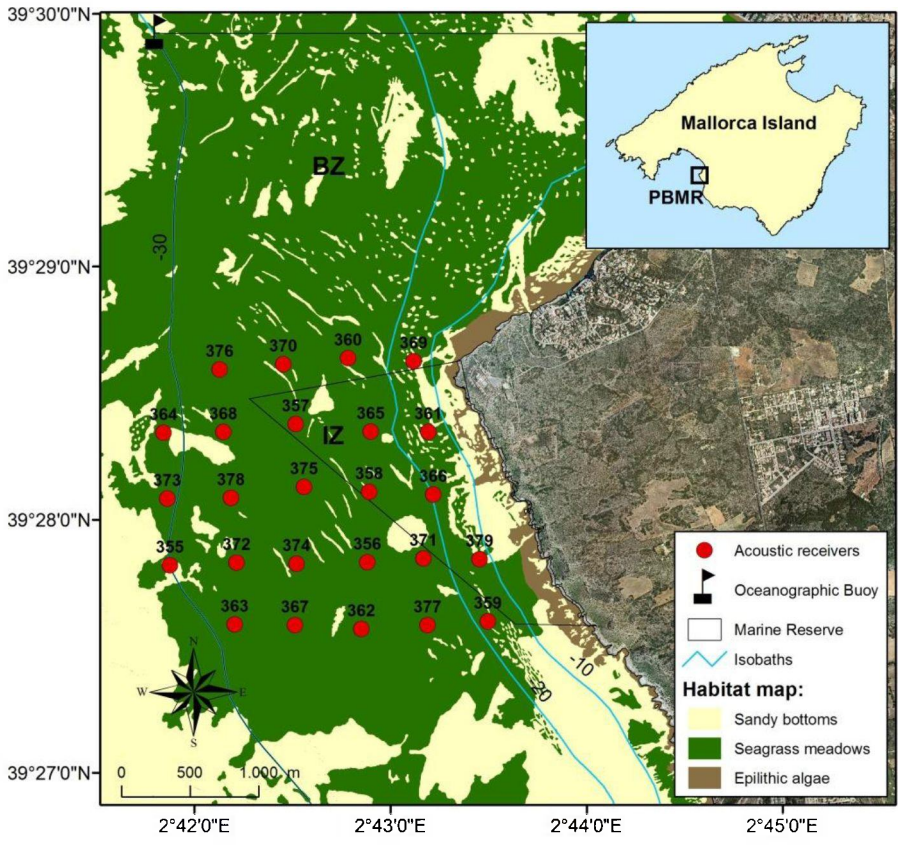


Figure 4.1 Palma Bay Marine Reserve (PBMR). Habitat map showing the locations of the acoustic receivers. Marine reserve boundaries enclose the Integral Zone (IZ) and the Buffer Zone (BZ).

4.2.2 Acoustic monitoring system

We used a fixed array of acoustic monitoring stations (Sonotronics, SUR-1) to track the movement of *S. scriba*. This system used small multifrequency, omnidirectional receivers, that measured and recorded the interval period between successive pings from individual transmitters. We used cylindrical ultrasonic transmitters (Sonotronics, PT-3, 19 mm in length, 7.8 mm in diameter, 1g in water, 21 days lifetime). Each transmitter emitted a continuous acoustic signal with a unique combination of frequency (ranging between 69 kHz and 83 kHz) and interval periods between pulses (ranging between 860 ms and 1250 ms), to allow for the identification of individual fish. Transmitters were turned on for 24 h d^{-1}, except four transmitters that were programmed to run intermittently to yield an active period of 12 h d^{-1} in order to increase the battery lifetime to approximately 35 days. Those transmitters runned their set of pulses twice,

and then added a period of silence for the same amount of time. Each successful signal detected by a receiver was recorded as a unique register with information regarding the date, time, frequency and interval period.

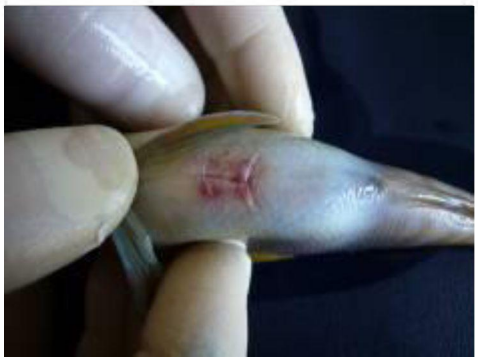


Figure 4.2 Detail of the sutures in an individual of *S. scriba*

4.2.3 Receiver deployment

In July 2007, we deployed 25 receivers within the study site, approximately 450 m from each other, covering a monitoring area of approximately 5 km^2 (Figure 4.1). We oriented upwards each receiver at 1-2 m from the bottom to optimize detections for demersal fishes and avoid thermocline effects (Figure 4.3). Receivers were placed at depths from 15 to 35 m, where the range of detection was up to ≈250 m (see Box 4.1). The receiver array allowed fish to be monitored for most of the period that they were within the detection range of the receiver array. We retrieved receivers, downloaded data, cleaned off biofouling organisms and redeployed the receivers three times (in September 2007, November 2007 and February 2008).

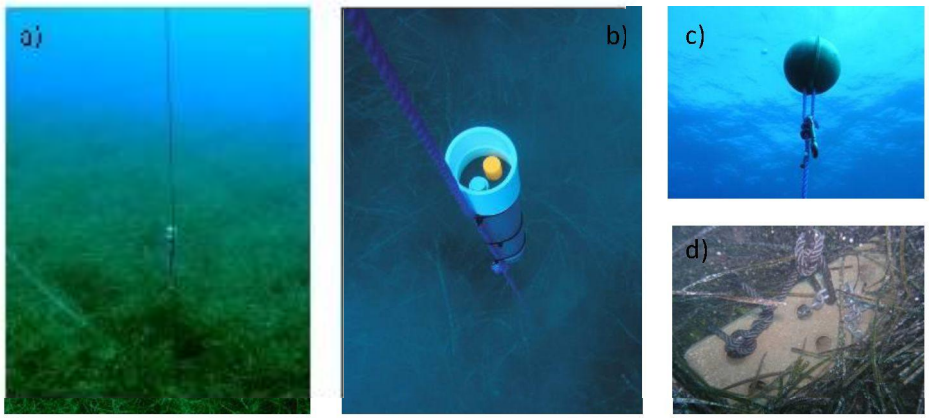


Figure 4.3 Deployment system: a) receiver oriented upwards over seagrass meadows; b) detail of the receiver with the acoustic transductor (in orange); c) sub-surface buoy allocated at 5-8 m depth for ease of the recovery of the system; d) weight mooring (≈20 kg in water).

4.2.4 Fish tagging

We released 15 tagged individuals of *S. scriba* from July 2007 to December 2007 (Table 4.1). Tagged fish were reproductively mature and were collected after the spawning season (Bauchot 1987a). Fish were captured during the daytime within the study area with a hook and line using large J-hooks. To avoid internal injuries from swim bladder expansion, fish were captured at depths between 10 and 25 m and, if necessary, were punctured with a hypodermic needle to release trapped gasses (Alós 2008). After capture, fish were transferred immediately to fresh seawater tanks following a procedure similar to that used for small fish (Jadot et al. 2006). Fish were anaesthetised with a solution (100 mg l^{-1}) of tricaine methanosul-

fate (MS222). After being fully anaesthetized, they were weighed to the nearest g and measured to the nearest mm (total length). Transmitters were surgically inserted into the peritoneal cavity and the incision was closed using synthetic absorbable sutures (Figure 4.2). Transmitters did not exceed 1.7% of the body weight of the fish. The surgery process took less than 5 min. A preliminary evaluation of the surgical procedure using 'dummy' transmitters with 6 individuals revealed normal behaviour 8-10 min after surgery, full cicatrisation without transmitter loss after 6 weeks, and 100% survival after 6 months (Grau unpubl. data). Following full recovery in a seawater tank, fish were released in good condition in the middle of the array to guarantee initial detection.

Table 4.1 *Serranus scriba*. Summary of the monitoring data for the 15 tagged fish. TL, total length; TP, total period between the release date and last detection; DD, number of days detected; and R_I, residence index.

Fish code	TL (mm)	Weight (g)	Release date (yy/mm/dd)	TP (d)	DD (d)	R_I	Total detections	No. of receivers
2	184	62.1	07/09/17	27	26	0.96	4475	9
3	169	66.2	07/09/26	29	29	1.00	5560	1
5	184	83.3	07/09/17	6	6	1.00	1179	1
18	173	61.0	07/09/17	36	35	0.97	2242	1
19	172	63.5	07/09/26	5	5	1.00	504	4
20	169	66.2	07/09/26	30	30	1.00	1037	4
35[a]	183	81.02	07/12/17	9	9	1.00	168	4
106[a]	193	89.32	07/12/17	1	1	1.00	41	1
123	179	68.9	07/07/26	5	5	1.00	2930	8
131	180	70.3	07/08/30	9	9	1.00	2580	7
138[a]	172	73.83	07/12/14	7	7	1.00	201	4
160	217	136.4	07/12/17	2	2	1.00	107	4
172[a]	197	92.68	07/12/14	27	8	0.30	314	3
190	177	73.08	07/12/17	5	5	1.00	192	3
200	175	74.07	07/12/14	4	4	1.00	466	5

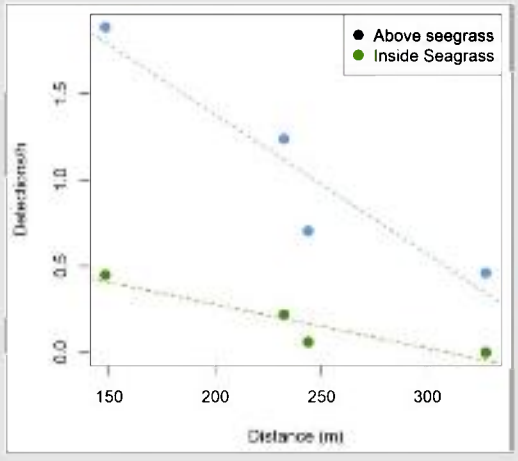
[a] Fish tagged with transmitters that were programmed to run intermittently to yield an active period of 12 h d^{-1}

Box 4.1 Effect of seagrass canopy on data logging acoustic receivers

An preliminary experimental test was conducted to assess the range of detection and evaluate the effect of seagrass canopy on acoustic transmissions.

We deployed two pairs of transmitters placed at different distances (range 150-330 m) from two different receivers. For each pair, we positioned one tag inside the seagrass canopy (leaf length ≈ 52 cm) and another one above. One pair of transmitters was deployed for 44 h, whereas the second pair remained for 66 h.

The total number of detections per hour was plotted against distance. The figure on the right indicates that detection range decreased above ≈250 m and seagrass canopy attenuated the number of received detections.



4.2.5 Data analysis

We designed and developed a MS Access database to store and manage detection data (Box 4.2). We matched each recorded detection with a unique individual by the frequency and the interval period between pulses using a tolerance of 5 ms (see Sonotronics Unique Pinger ID Algorithm. Accessed 24 May 2014. http://sonotronics.com/wp-content/uploads/2010/07/PingerAlgorithm.pdf). We then filtered our data to remove potentially spurious detections. We defined spurious detections as any single transmitter code detection occurring alone within a 24 h period. We developed a decision tree diagram to formalize the process of fish selection for the different analyses, where we took into account: (1) the number of receivers detected, (2) the detection period, and (3) the results of both temporal and spatial analyses. All spatial and statistical analyses were performed with a custom program written in R (R Foundation; http://www.r-project.org).

Box 4.2 SURDB (SUR-1 Database Management System)

SURDB is the information system developed to manage and analyze acoustic tracking data from acoustic listening stations (Sonotronics, SUR-1). This system has been developed as part of this thesis due to the lack of software being able to response all our analytical requirements. The core of the system is a relational database management system (RDBMS) implemented in MS Access. The database stores information uploaded from the receivers together with information for each tagged individual (i.e., biological characteristics and information from the tagging procedure). Then, data is processed, summarized and analyzed using Structured Query Language (SQL). In addition, connection from other software is also possible through OBDC (Open Database Connectivity) drivers. Specifically, a complete suite of R scripts, also developed in this thesis, connect the database and use the information for computing spatial and temporal analysis (e.g. estimates of home range size or continuous wavelet transform). Similarly, different GIS tools (e.g. ArcMap, QGIS) can also access the georeferenced information and visualize in digital maps.

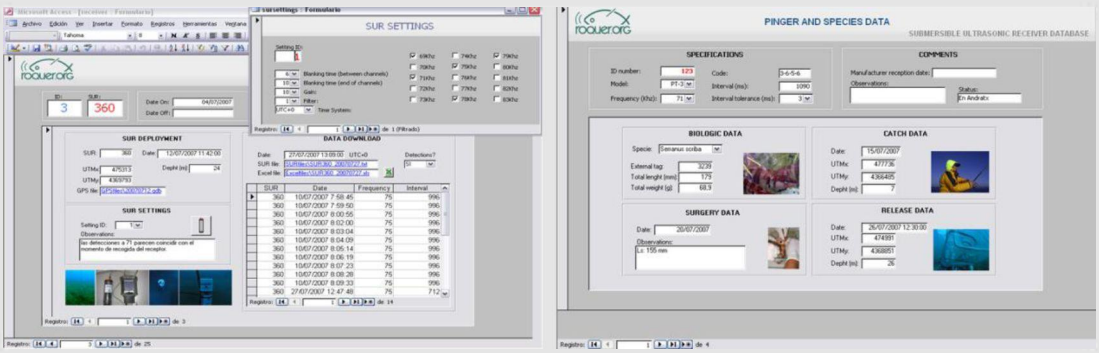


Figure 4.4 SURDB interface with receiver data (left panel) and relevant information about the tagging procedure (right panel).

4.2.5.1 Residence time

We plotted daily presence histories to visually inspect the timeline of fish presence. We calculated the total period between the release date and the last detection (TP), as well as the number of days detected (DD). We used both types of data to calculate a residence index (R_I), defined as the quotient between the DD and the TP. In contrast to Abecasis and Erzini (2008), we estimated R_I for each fish, rather than for each receiver, and used it as an alternative to determining the number of consecutive days of presence (Collins et al. 2007). We used a Pearson's correlation test to evaluate differences in TP, DD and R_I with fish size.

4.2.5.2 Temporal patterns

Temporal patterns were analysed for fish that were detected for 5 days or more. We pooled the detections of all receivers into hourly bins for each fish, and visually inspected the data using chronograms. Then, we used the continuous wavelet transform (CWT) to identify periodicity patterns in *S. scriba* detection hourly bins. The CWT is a powerful tool for decomposing a time series into time-frequency space (Percival and Walden 2000), which has been previously applied on data storage tags (Subbey et al. 2008). We computed the two-dimensional wavelet spectrum and pointwise test (95% significance level) using a Morlet wavelet with the *sowas* package in R (Maraun et al. 2007). Wavelet coefficient values were normalized such that the highest spectral power equalled one. Finally, we investigated diel patterns by binning hourly detection data for each individual into daily phases (day/night) and then comparing mean detections in each phase bin. We defined each phase using sunrise and sunset data obtained from the U.S. Naval Observatory (Astronomical Applications Department; Accessed 26 May. http://aa.usno.navy.mil/). Diel data were non-normally distributed, and could not be transformed adequately. We used a non-parametric Mann-Whitney U-test to evaluate the hypothesis that the number of detections was different between day and night.

4.2.5.3 Spatial patterns

Spatial movement patterns were analysed for fish that were detected at more than one receiver. We used the Nadaraya-Watson normal-kernel estimator with the *sm* package in R (Bowman and Azzalini 1997) to calculate position estimates, or "centre of activity" locations (COA), for monitored fish every 60 minutes (see Simpfendorfer et al. 2002, Hedger et al. 2008). Processed data were used for all of the following analyses.

For comparison, we estimated the home range over the total period of detection using two methods: (1) Minimum convex polygons based on 100% of the positions (MCP 100); and (2) bivariate normal fixed kernel utilization distributions (95% and 50% KUD). MCP provided information regarding the extent of an animal's range over a given period, while KUDs provided information regarding the use of space within that range including core area (50% KUD) and home range (95% KUD). We calculated MCP and KUDs over a grid of 15 x 15 m resolution using the *adehabitat* package in R (Calenge 2006). We selected a kernel bandwidth of 250 m, corresponding to the detection range of the transmitter. To determine whether the home range size was related to residence time or fish size, we compared total MCP and KUDs to the total period of detection (TP) and fish size (TL) using the Pearson's correlation test.

We investigated changes in home range over time based on 95% KUD. Observation-area curves were calculated by plotting cumulative home ranges over a period of days. We assessed when an asymptote was reached as the point when the percent change of the accumulated area was less than 5% (Rechisky & Wetherbee 2003). For every fish, the percent change for each tracking day was calculated as:

$$\% \text{ change} = [(A_t - A_{t-1}) / A_t] \times 100 \quad \text{(Equation 4.1)}$$

where A_t is the 95% KUD area at day t, and A_{t-1} is the 95% KUD area at the previous day, t – 1. We only reported total home range estimates for fish for which the home range approached an asymptote, as recommended by Laver and Kelly (2008).

We calculated two measurements of site fidelity: (1) the Linearity index (LI); and (2) the Index of Reuse (IOR; Rechisky and Wetherbee 2003). The Linearity index was calculated as follows:

$$LI = (F_n - F_1) / D \quad \text{(Equation 4.2)}$$

where $F_n - F_1$ is the distance between the first and last COA, and D is the total distance travelled. Fish with nomadic behaviour should have LI values close to 1, while fish with strong site fidelity should have an LI value approaching 0. The IOR is calculated as:

$$IOR = [OV(A_1,A_2)] / [UN(A_1,A_2)] \quad \text{(Equation 4.3)}$$

where $[OV(A_1,A_2)]$ is the area of overlap between two activity spaces (i.e., daily 50% and 95% KUD areas), and $[UN(A_1,A_2)]$ is the area of union of both activity spaces. An IOR = 1 indicates a complete overlap of activity space (site fidelity), while an IOR = 0 indicates non-overlap of activity space (nomadic behaviour).

To test for diel differences in home range size and home range shift for all fishes, we calculated: (1) daytime and night-time KUDs on a daily basis; and (2) the IOR between total daytime and night-time activity spaces. Paired t-tests were used to detect differences between day and night on the home range patterns for each fish.

4.3 Results

Between June 2007 and January 2008, 16 (64%) of the 25 receivers detected all of the 15 released fish. Fish detections are summarized in Table 4.1. The total number of detections ranged from 42 to 317 detections for fish with tags programmed to run for 12 h d^{-1}, while for tags that run 24 h d^{-1}, the number of detections ranged from 107 to 5,514.

The generated decision tree diagram is presented in Figure 4.5. One tagged fish (#106) was excluded from all analyses, as it was only detected by one receiver on only a single day and with just 41 detections. Battery failure, death, capture by fishermen or predation by other animals could be the reason for that pattern. Two more fish (#200 and #160) were excluded from temporal analyses as they were detected for a period of less than 5 d; while three other fish (#3, #5 and #18) were excluded from spatial analysis because they were detected by only one receiver.

4.3.1 Residence time

Short-time residence differed among tagged fish (Figure 4.6). Some fish were not detected beyond a few days post-release, while others remained within the study area for a longer time period. Two fish were initially released in July and August, whereas the others were released in two groups. The first group contained six fish and was released in September, while the second group contained seven fish and was released in December. Total periods of fish presence ranged between 1 to 36 days (Table 4.1). The mean total monitoring period for all *S. scriba* was 13 d. The R_I scores resulted in high values (0.95 ± 0.18, mean ± SD), indicating a continuous presence of fishes through the total period of detections within the monitoring area. However, fish #172 presented a high intermittent detection pattern, resulting in the lowest R_I (0.3). This pattern was demonstrated after the fish moved out from the monitoring area 4 days after the release date and reappeared intermittently. There were non-significant correlations between fish size and residence time measures (r^2 = -0.25 for total residence time, n = 14, p = 0.327; r^2 = -0.42 for number of days detected, n = 14, p = 0.137; r^2 = -0.36 for R_I, n = 14, p = 0.203).

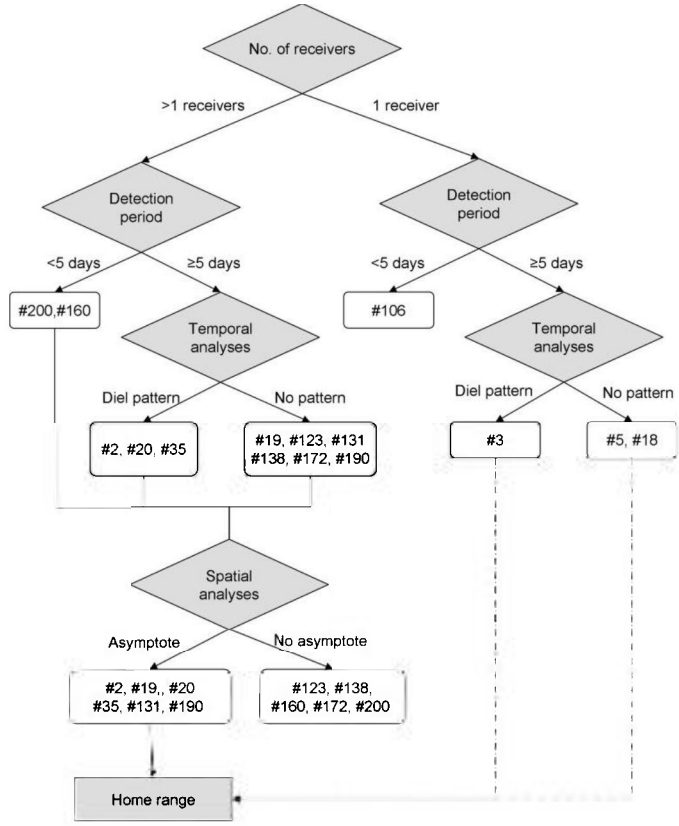


Figure 4.5 *Serranus scriba*. Decision tree diagram used to select fish for reporting home range sizes.

4.3.2 Temporal patterns

Chronograms of hourly detections revealed a diel pattern for some fish, with a higher number of detections occurring during the daytime than at night (Figure 4.7). However, this pattern was not constant throughout the detection period, and was not evident for all fish. Oceanographic features, such as water conductivity, did not show a correlation with the number of detections (Figure 4.7). The use of CWT allowed the identification of periodicities in time series of detection data. Of the 12 fish analysed, 4 (33.3%) presented clear periodicities of 24 h in their wavelet spectrograms (Figure 4.8). Fish #2 and #20 also presented significant patches in the 12 h scale within a more localized timeframe, which could be the

result of a crepuscular cycle or an increment of the number of detections at midnight. In addition, fish #20 also showed a significant patch at the 48 h scale. As the 48 h patch occurred at the same time than the 24 h patches, it was likely to be the second harmonic of the 24 h scale. All 12 fish presented a higher mean number of detections during the daytime than at night (Table 4.2). However, only the four fish with 24 h periodicities identified by CWT presented significant differences (Mann-Whitney U-test, $p < 0.05$; Table 4.2).

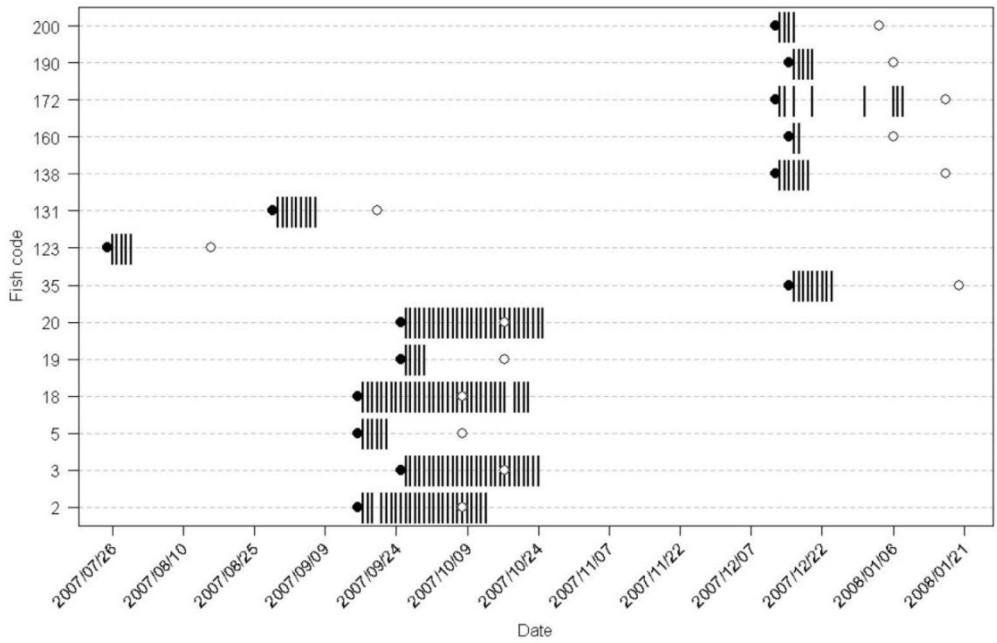


Figure 4.6 *Serranus scriba*. Abacus plot of daily presence (vertical lines = dates detected) of tagged individuals within the monitoring area between July 2007 and January 2008. (●) Transmitter deployment dates; (○) predicted transmitter death dates.

4.3.3 Movement patterns

Asymptote analysis based on observation-area curves are presented in Figure 4.9. Five fish (#123, #138, #160, #172 and #200) increased their home ranges without reaching an asymptote (Table 4.3). Their estimated paths indicated that those fish moved toward the boundaries of the monitoring array over a short period. After that period, the fish were no longer detected, with the exception of fish #172, which was intermittently detected at the receivers located at the boundaries. The other six fish (#2, #19, #20, #35, #190, #131) also increased their home ranges during the first days, but then stabilized their home range size, reaching an asymptote based on the 5% change criteria. The period for stabilization ranged between 3 and 6 days (Table 4.3). After that period, home range size was stable, except for fish #2 and #19, whose home range size decreased due to the repeated use of their activity space (Figure 4.9a). No significant differences were found between fish groups (with and without asymptote) and fish TL (t-test, d.f. = 6, $p = 0.579$).

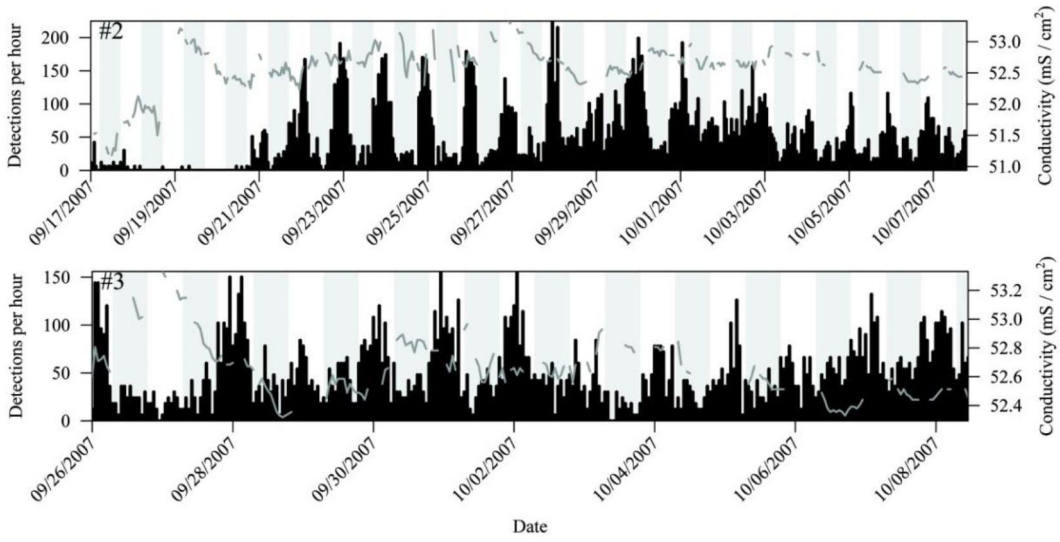


Figure 4.7 *Serranus scriba*. Time plots of hourly detection bins (vertical black histograms) and water conductivity (gray line) of two individuals. Vertical stripes of shading show night-time periods. An approximately 24 h pattern oscillation is evident in fish #2 and #3, with a higher number of detections occurring during daytime.

Home range sizes (95% KUD and MCP) and core areas (50% KUD), are presented in Table 4.3, while some examples are plotted in Figure 4.10. We did not report home range estimates for fish that did not reach an asymptote. The total home range obtained with 95% KUD ranged between 0.760 km^2 and 1.333 km^2, with a mean size of 1.108 km^2, whereas total home range obtained with MCP ranged between 0.102 km^2 and 0.671 km^2, with a mean size of 0.248 km^2. The total home range size estimated with MCP was significantly smaller than that obtained with 95% KUD (t-test paired for means, $t = 8.346$, d.f. = 5, $p < 0.001$). The core area ranged between 0.175 km^2 and 0.294 km^2, with a mean size of 0.241 km^2. Total home range areas did not exhibit a significant relationship with fish TL ($r^2 = 0.71$ for MCP, $n = 6$, $p = 0.116$; $r^2 = 0.66$ for 95% KUD, $n = 6$, $p = 0.155$) or with the track duration ($r^2 = 0.46$ for MCP, $n = 6$, $p = 0.363$; $r^2 = -0.57$ for 95% KUD, $n = 6$, $p = 0.241$).

Linearity index values were low for most of the fish, but were highly variable, with a mean of 0.326 ± 0.308 (± SD; Table 4.3). Higher values were found in fish whose home range did not reach an asymptote (0.582 ± 0.252, mean ± SD), indicating that movements tended to be unidirectional. Lower values corresponded to fishes that reached an asymptote (0.112 ± 0.135, mean ± SD), indicating little movements from the area with a repeated use of the activity space. We compared LI values between fish with and without asymptotes in their home ranges and found significant differences (t-test, d.f. = 6, $p = 0.010$). IOR values were higher (Table 4.3), and negatively correlated with LI ($r^2 = -0.60$, $n = 11$, $p = 0.053$). IOR values based on a 95% KUD daily shift were higher (0.81 ± 0.26, mean ± SD), than those based on a 50% KUD (0.76 ± 0.33, mean ± SD).

Tracked fish did not exhibit any detectable diel pattern in home range size or home range shift. There were no differences for any fish between day and night based on both 95% KUD and 50% KUD (t-test, p >

0.05). When comparing total home range areas during the day and night for each fish, IOR values for 95% KUD were higher (0.76 ± 0.21, mean ± SD) than for 50% KUD (0.58 ± 0.37, mean ± SD).

4.4 Discussion

4.4.1 Residency and site fidelity

Tracked fish were detected within the monitoring area for varying lengths of time, and usually through consecutive days. This suggests a continuous use of the monitoring area through the detected period. Only one fish (#172) presented a transient use of the study site. As intermittent detections of this fish were received by a monitoring station located in the boundaries of the array, the loss of contact with this fish could be the result of movement out of the study area. Five of the 15 tagged fish were monitored for more than 25 days, suggesting a consistent pattern of residence. However, the majority of tracked fish were monitored for shorter periods due to the loss of their detections. In other studies conducted with bigger Serranids and long-life transmitters or conventional external tags, longer time residence periods were reported for *Plectropomus leopardus* (202 d; Zeller 1997), *Epinephelus guttatus* (54-143 d; Shapiro et al. 1994), *Epinephelus tauvina* (5-105 d; Kaunda-Arara and Rose 2004) and *Paralabrax clathratus* (3 yr; Lowe et al. 2003). The limitation of battery lifetime is an important factor when considering residence time. As in our study, this factor is relevant when working with small fish, as battery lifetime is directly proportional to transmitter size. Thus, in our study, we could only evaluate short-time residence due to the small size of *S. scriba*.

4.4.2 Diel patterns

Results suggest diel patterns for some individuals of *S. scriba*, though this pattern was not observed on all fishes. Constant diel patterns for all fish were reported by other authors (Topping et al. 2005, Jorgensen et al. 2006), though intraspecific variability was also found in *Sarpa salpa* (Jadot et al. 2006).

Table 4.2 *Serranus scriba*. Temporal analysis of 12 tagged fish. W values correspond to a Mann-Whitney U-test. * $p < 0.05$; ** $p < 0.01$; and $^{n.s.}$ not significant

Fish code	Daytime detections (mean ± SD)	Night-time detections (mean ± SD)	W
2	118 ± 79	48 ± 38	159.5**
3	119 ± 61	73 ± 37	173.0**
5	105 ± 54	91 ± 51	21.0$^{n.s.}$
18	33 ± 36	31 ± 25	644.5$^{n.s.}$
19	64 ± 59	36 ± 21	8.5$^{n.s.}$
20	23 ± 19	11 ± 8	205.0**
35	16 ± 13	5 ± 4	8.0*
123	385 ± 219	201 ± 185	8.0$^{n.s.}$
131	155 ± 66	132 ± 80	41.0$^{n.s.}$
138	19 ± 21	10 ± 15	15.5$^{n.s.}$
172	24 ± 38	11 ± 18	22.5$^{n.s.}$
190	25 ± 23	13 ± 26	4.0$^{n.s.}$

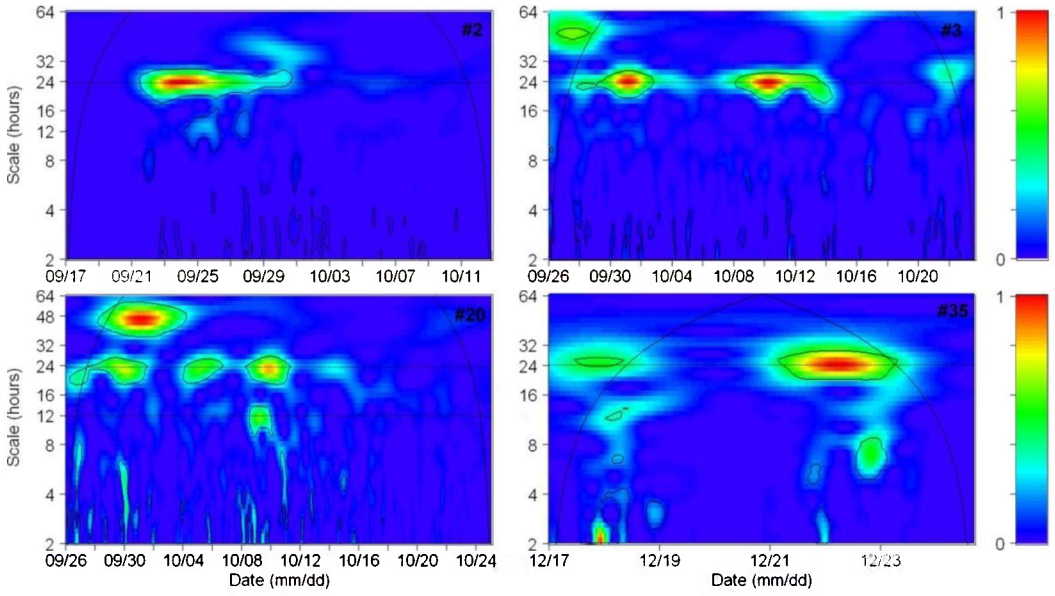


Figure 4.8 *Serranus scriba*. Wavelet sample spectrums of fish #2, #3, #20 and #35 using a Morlet wavelet. Horizontal dashed line represents the 12 h, 24 h and 24 h scales. Continuous thin lines represent the cone of influence (COI). Values outside the COI should not be interpreted due to edge effects. Thick contours represent the 95% confidence level.

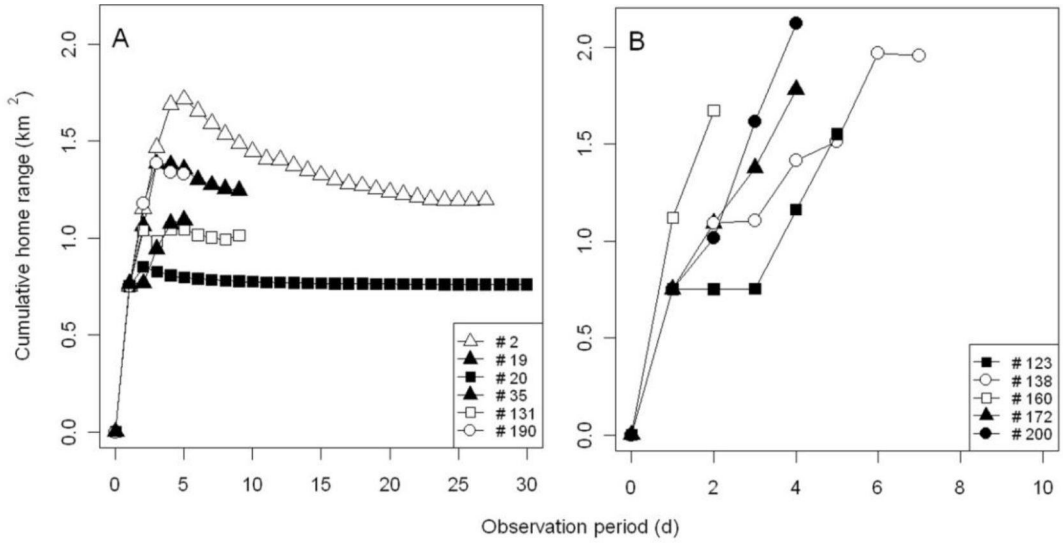


Figure 4.9 *Serranus scriba*. Observation-area curves for 11 fish tracked in Palma Bay. (A) Individuals whose 95% KUD reaches an asymptote, indicating that activity space increased little with additional tracking time; and (B) Individuals whose 95% KUD increases more than 5% between consecutive tracking days and does not reach an asymptote.

Table 4.3 *S. scriba*. Movement statistics: MCP, minimum convex polygon; KUD, kernel utilization distribution; and IOR, Index of Reuse. IOR values are estimated with 95% KUD. Asymptote values correspond to the period used for each fish to reach an asymptote in their accumulated home range area (95% KUD) based on the 5% change criteria. Total home range estimates were not reported for fish that did not reach an asymptote.

Fish code	MCP (km^2)	95% KUD (km^2)	50% KUD (km^2)	Asymptote (d)	L_i	Daily IOR (mean ± SD)	Day-Night IOR (mean ± SD)	95% KUD daytime (km^2)	95% KUD Night-time (km^2)
2	0.671	1.197	0.215	5	0.015	0.81 ± 0.19	0.95	1.204	1.189
19	0.116	1.092	0.267	5	0.177	0.76 ± 0.21	0.76	0.955	1.130
20	0.102	0.760	0.175	3	0.000	0.99 ± 0.04	0.99	0.761	0.759
35	0.214	1.248	0.273	4	0.143	0.84 ± 0.25	0.82	1.100	1.320
123	-	-	-	-	0.311	0.69 ± 0.36	0.74	1.528	1.391
131	0.248	1.015	0.223	5	0.000	0.74 ± 0.11	0.86	1.064	0.938
138	-	-	-	-	0.643	0.59 ± 0.37	0.77	1.902	1.827
160	-	-	-	-	0.795	0.16[a]	0.22	1.498	1.341
172	-	-	-	-	0.839	0.78 ± 0.42	0.89	1.678	1.774
190	0.135	1.333	0.294	4	0.340	0.61 ± 0.18	0.72	1.141	1.487
200	-	-	-	-	0.325	0.38 ± 0.29	0.68	2.102	1.896

[a] Value estimated with only one measure.

The diel pattern in the number of detections of acoustic transmitters could be influenced by several factors. Based on temporal series data from the oceanographic buoy, we excluded the effect of diel variability of different water parameters such as temperature, salinity or conductivity that could affect transmission attenuation. Other authors have detected diel shifts in the home range to different habitats (Jadot et al. 2006), and found a negative relationship between detection frequency and rate of movement (Topping et al. 2006), or that higher number of detections during the day were related with periods of activity (Zeller 1997). However, in our study, we did not detect diel differences in horizontal movement patterns. A possible explanation for the diel frequency of detections could be based on the behaviour of *S. scriba* in relation with the structure of the dominant habitat type, *P. oceanica* meadows. Seagrasses have a significant effect on sound propagation due to their lacunar air system, which could produce high levels of transmission loss (Miksis-Olds and Miller 2006). A comparative test between transmitters positioned inside and above *P. oceanica* indicated that tags inside seagrass canopy could decrease the number of detections down to >80% (Box 4.1). Therefore, if during the night *S. scriba* hid under the canopy of the seagrass, the number of detected signals should be lower at night. This diel pattern could be supported by different studies that reported: (1) significantly lower abundance estimates of *S. scriba* during the night (Reñones et al. 1995, Azzurro et al. 2007), and (2) a diurnal feeding activity of a similar species, *Serranus atricauda* (Morato et al. 2000). These findings would suggest that *S. scriba* could exhibit a differential behaviour with a high activity period during the day (i.e., swimming and predating over the seagrass), and a resting period during the night (i.e., due to food partitioning with nocturnal competitors such as *Scorpaena porcus*; Arculeo et al. 1993). Although this explanation is plausible, the intraspecific variability and the short temporal duration of this study makes it difficult to identify concrete causal mechanisms. Further research using laboratory-oriented experiments (Reebs 2002), could be used to examine the factors associated with such plasticity.

The implications of diel patterns are also important in relation to the criteria used to include or discard fishes for analyses (Figure 4.5). It is common to consider dead fish by continuous detection at a single receiver (e.g., Taylor et al. 2006). In our study, fish #3 was continuously detected by only one receiver

over 29 d, but exhibited a diel pattern in the number of detections in contrast with individuals #5 and #18. Based on our interpretation of a differential behaviour in relation with seagrass structure, it would be possible that fish #3 could be alive. That fish would exhibit a similar behaviour to the other individuals with diel patterns that were detected at more than one receiver, but moving within a more reduced activity space

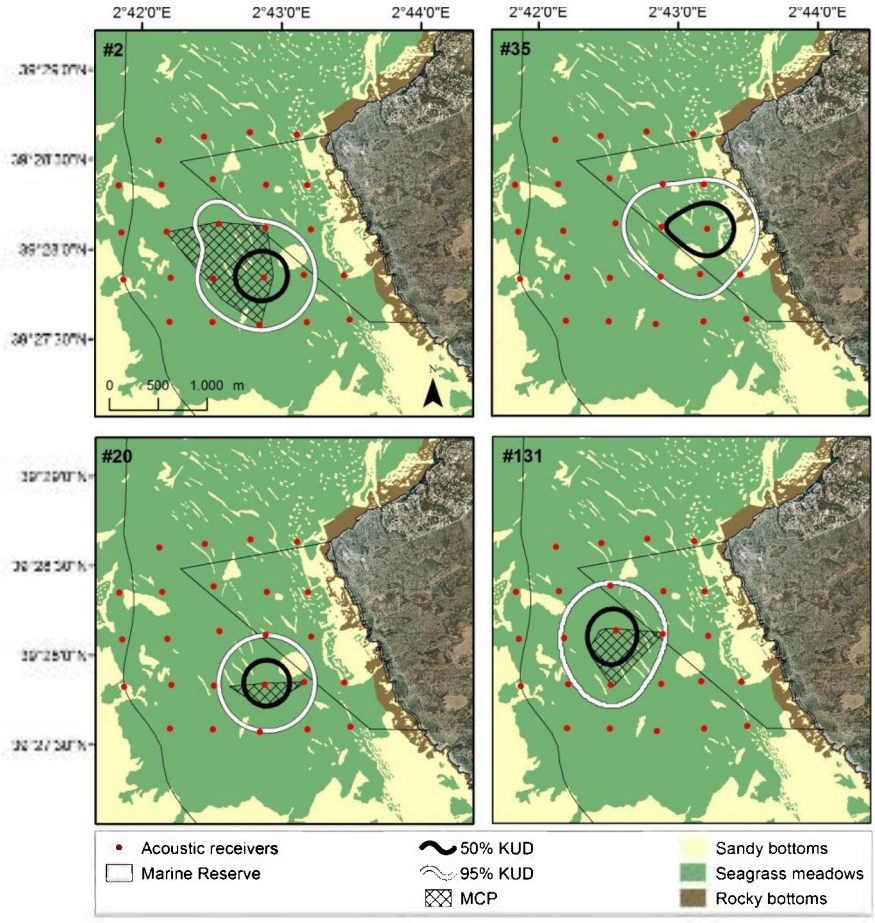


Figure 4.10 *Serranus scriba*. Total home range areas (MCP and 95% KUD) and core areas (50% KUD) for four individuals tracked within the monitoring area.

4.4.3 Movement patterns

Our findings support several common assumptions about *S. scriba* behaviour. Based on direct observations, *S. scriba* has been described as a sedentary and territorial species, suggesting a limited dispersal capacity (Bauchot 1987a, Harmelin 1987). In addition, our findings revealed intraspecific variability. Adult individuals of *S. scriba* exhibited both resident and mobile behaviour. Resident fish presented a

higher site fidelity in a smaller area without daily shifts, while non-resident fish tended to exhibit more linear movements. IOR were high, although the available area for fish was extensive.

Home range size estimates are highly dependent upon the method used. MCP estimates tend to overestimate home ranges because they are affected by peripheral locations. However, when individuals use a relatively limited space, kernel areas can be even higher than those of MCP (Rechisky and Wetherbee 2003). In our study, the selection of kernel bandwidth allowed us to incorporate the uncertainty of positional errors into home range estimates. The resulting spatial accuracy did not allow fine movements to be determined at a small scale that would correspond with microhabitat preferences. However, the design of the array allowed us to identify different patterns of movement, from highly resident movements to more nomadic behaviour.

Our results contrast with other studies conducted with other Serranid species with a larger body size. Home range estimates for *S. scriba* were higher than those reported for *Plectropomus leopardus* (10458.4 - 18796.9 m^2, Zeller 1997), *Epinephelus guttatus* (112 - 5636 m^2, Shapiro et al. 1994) and *Paralabrax clathratus* (33 - 11224 m^2, Lowe et al. 2003), while they were within the range of movement estimated for *Epinephelus tauvina* (70000 - 730000 m^2, Kaunda-Arara & Rose 2004). If we take into account the fact that smaller Serranids may have a weaker relationship with bottom features on a microhabitat scale than larger Serranids (La Mesa et al. 2002), it is plausible that the home range of *S. scriba* could be even higher than that of bigger Serranids.

S. scriba presented intraspecific variability both in temporal and spatial patterns. The detection of diel patterns should be taken into consideration when designing monitoring surveys to estimate abundance for this species. Moreover, the small home range of *S. scriba* supports the use of this fish as a bioindicator of human impacts (e.g., marine pollution or recreational fishing overexploitation). Home ranges of resident adult *S. scriba* were intermediate (average 12.4 % according to MCP; 55 % according to 95% KUD) in relation to the size of the integral zone of the PBMR, and small (average 0.01 % according to MCP; 0.05 % according to 95 % KUD) in relation to the buffer zone of the PBMR. In addition, our data suggest that 36% of the fish studied exhibited a more mobile behaviour. Limitations to determine whether those fish relocated beyond the monitoring area or the MPA do not allow to clearly demonstrate a net export to adjacent fishing grounds. However, our data support the hypothesis that PBMR could benefit the adjacent fished areas. If the fish tracked and home range sizes determined in this study were representative of other adults within the PBMR and over longer periods, then it is likely that: (1) the size of the integral zone would be enough to contain a high proportion of the regular movements of *S. scriba*, but also allow cross-boundary movements to the buffer zone; (2) the size of the buffer zone could be effective in recovering the resident adult stock of *S. scriba*, but would restrict adult spillover to the areas close to reserve borders. Further research addressed to integrate spatially explicit models of fishing effort and fish abundance within PMBR would refine the understanding of processes such as spillover.

Our results provided new information regarding the biology of *S. scriba*. Future long-term monitoring studies aimed at determining residence over extended periods through heterogeneous habitat would further improve our understanding of spatio-temporal patterns and habitat requirements of *S. scriba*, and the implications of these studies would provide a better assessment of the recreational fishery and the management of MPAs.

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Chapter 5
Movement patterns of *Diplodus annularis*

Abstract

In this Chapter, the short-term movements of a small temperate fish, the annular seabream *Diplodus annularis* (Linnaeus 1758), were examined using standard tag-recapture and passive acoustic telemetry in PBMR. All the fish tagged with standard tags were recaptured near the release locations, with a maximum distance of ≈300 m. The maximum time between release and recapture was 185 d. Two different arrays of acoustic receivers were deployed, one in 2008 and another in 2009, within PBMR. Twenty adults were surgically tagged with acoustic transmitters. Fish monitored in 2008 (n = 12) were translocated from the point of capture to analyse the movement behaviour after artificial displacement. Upon release at displaced locations, 67% of the fish moved towards the original capture location using a time of return that ranged from 0.75 to 15.25 h. Fish monitored in 2009 (n = 8) were released at the point of capture. They showed high site fidelity with a maximum period of 27 d between the first time and the last time they were detected. The results of this study provide valuable information for assessing the recreational fishery, suggesting that MPAs can be used to protect the adult stock of *D. annularis*, and highlighting the potential use of this species as bioindicator of local impacts.

5.1 Introduction

Results from the previous Chapter showed that passive acoustic telemetry systems performed well in a marine environment like Palma Bay, and current technology is appropriate for tracking small fish. Another species also targeted by the 'roquer' fishery is the annular seabream, *Diplodus annularis* (Linnaeus 1758). *D. annularis* is a littoral benthic fish, common in the bottoms covered by seagrass beds from 0 to 50 m depth (Bauchot 1987b). This small Sparid inhabits the Mediterranean and Black Sea coast, the Atlantic from the gulf of Biscay to Gibraltar, and the Madeira and Canary Islands (Bauchot 1987b). It has been catalogued as a rudimentary hermaphrodite (Buxton and Garratt 1990, Alós et al. 2010b), with a spawning period between May and June (Alonso-Fernández et al. 2011). Total lengths (TL) at 50% maturity are 9.0 cm for males and 10.0 cm for females (Matic-Skoko et al. 2007). In the Balearic Islands (NW Mediterranean), *D. annularis* is one of the species most frequently targeted by recreational boat and shore anglers (Morales-Nin et al. 2005), and has a minimum legal size of 12 cm. Recent studies have used *D. annularis* to assess the impacts of recreational fisheries (Cardona et al. 2007, Alós et al. 2008). Thus, information on the movements of *D. annularis* is relevant for the management of recreational fisheries.

In this Chapter, we used both conventional external tagging and passive acoustic telemetry to examine the short-term movement patterns of a small temperate fish, the annular seabream *D. annularis*. The specific aims of the study were: (1) to quantify the short-term movement patterns of *D. annularis*; (2) to determine short-term site fidelity; and (3) to describe movement behaviour after artificial displacement.

5.2 Methods

5.2.1 Conventional tagging experiment

Conventional tagging was conducted in different tagging sessions between February 2007 and May 2007 in Palma Bay (Figure 5.1, lower inset). Fish were captured with hook and line using large J-hooks in order to reduce hooking mortality (Alós 2008). Only individuals displaying good physical condition (i.e., those without hooking injuries or evidence of barotraumas after 10 min of visual inspection) were selected to be marked. After capture, fish were tagged with external T-tags (Floy Tag) inserted bellow the dorsal fin and then released at the capture location. Each tag displayed an ID and a telephone number. Total fish length (to the nearest mm), date and time, capture depth (m) and geographic coordinates were recorded for each released individual. A specific communication program was designed and implemented to inform the recreational fishing community regarding the external tagging program (Cardona-Pons et al. 2010).

A preliminary study in tanks showed that mortality related to capture and tagging was negligible. In addition, the 35% of tagged individuals (n = 20) shed their tag after 19 d, but this percentage kept constant up to 50 d, when the experiment finished (Alós unpubl. data).

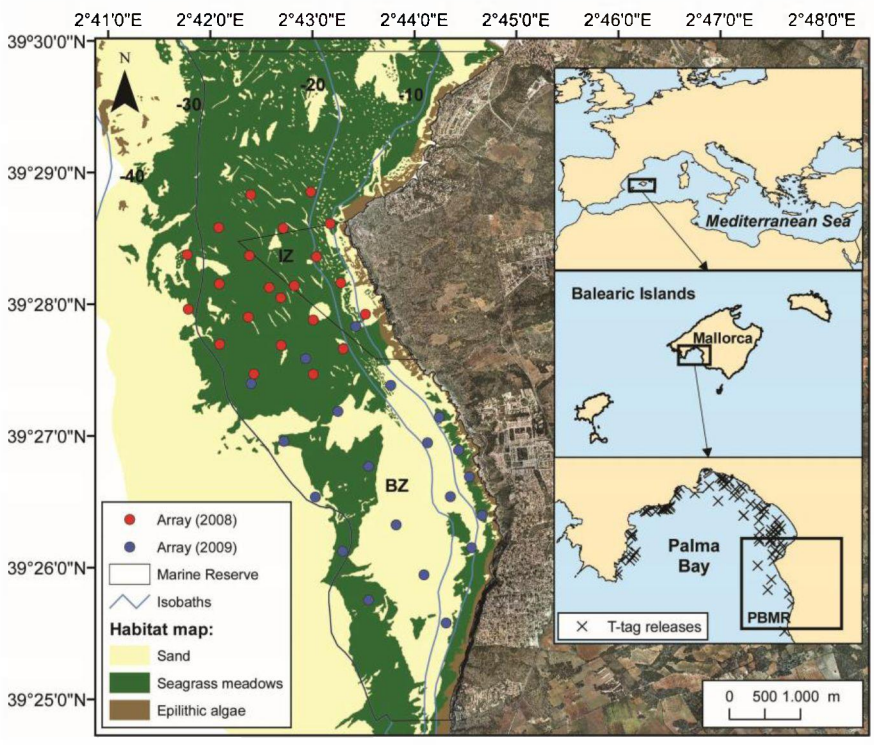

Figure 5.1 Map of the study area showing the locations of the acoustic receiver arrays for the years 2008 and 2009. Palma Bay Marine Reserve (PBMR) boundaries enclose the Integral Zone (IZ) and the Buffer Zone (BZ). The lower inset represents the locations of capture and release used in the conventional tagging experiment at Palma Bay.

5.2.2 Acoustic tagging

In addition, acoustic tagging was conducted in March-April 2008 and July-August 2009 in PBMR. We surgically tagged adult individuals (n = 20) with acoustic transmitters (Sonotronics, PT-3) following the procedure described in Chapter 4. We combined transmitters that were turned on for 24 h d^{-1}, with transmitters that yield an active period of 12 h d^{-1} in order to increase the battery life to approximately 35 d. Those transmitters were programmed to ran intermittently their set of pulses twice, and then added a period of silence for the same amount of time. Transmitters did not exceed 2.27% of the body weight of the fish. A preliminary evaluation of the surgical procedure using 'dummy' transmitters with 6 individuals showed normal behaviour 8 to 10 min after surgery, full cicatrisation without transmitter loss and 100% survival after 1 week (Grau, unpubl. data).

5.2.3 Receiver deployment

We used the same system of acoustic monitoring stations (Sonotronics, SUR-1) described in Chapter 4. Receivers were placed at depths from 10 to 35 m. Two different receiver arrays were used in PBMR (Figure 5.1). The first was deployed between March and April 2008 using 22 receivers and covering a monitoring area of approximately 4.7 km^2. The distance between receivers (≈500 m) allowed fish to be

monitored for most of the period that they were within the monitoring area. The main habitat found within this array was seagrass meadows of *P. oceanica*. The second array was deployed between July and August 2009 using 20 receivers and covered a wider area of approximately 7.5 km^2. The distance between receivers (≈900 m) meant that their ranges did not overlap. In this case, the habitat type was more heterogeneous, with both seagrass meadows and sandy bottoms.

5.2.4 Displacement experiment

We released tagged fish at the capture site, except those tagged with acoustic transmitters in 2008, which were displaced to a location ≈1500 m from the capture point. The release sites had a benthic habitat similar to the capture sites (i.e., seagrass meadow). We assessed whether a fish moved back to the capture location by recording the time that they were first detected by either one of the two receivers that were closest to the capture location.

5.2.5 Data analysis

We examined conventional tag-recapture data in order to determine the number of days and distance between capture and recapture locations. As fish were not released again, only single-tag recovery data was available for this study. For acoustic telemetry data, we used the Microsoft Access database and R program described in the previous Chapter (see Box 4.2) to manage and analyse the detection data downloaded from the receivers. The data was filtered to remove potentially spurious detections. We defined spurious detections as any single transmitter code detection that occurred alone within a 24 h period. Daily presence histories were plotted to inspect the fish presence timelines visually. We calculated the total period between the first and last detection (TP), the number of days detected (DD) and the residence index for each fish (R_I; see Section 4.2.5.1). For the 2008 array, in which detection ranges overlapped, we used the Nadaraya-Watson normal-kernel estimator to calculate the position estimates, or "centre of activity" locations (COA), as described in Section 4.2.5.3. Distances between consecutive 15 min COA locations were used to measure the linearity index (LI; see Equation 4.2).

5.3 Results

5.3.1 Tag-recapture

We tagged 1149 individuals of *D. annularis* with external T-tags. The total length (TL) ranged between 8.7 and 16.7 cm (Table 5.1). At the end of the project (August 2008) the recapture rate was low (1.31%), as only 15 fish were recaptured. Four (26.7%) of the fish were recaptured by the research team at tagging sessions, whereas 11 fish were recaptured by recreational anglers. In both cases, recaptures were conducted using hook and line. Most of the recaptures occurred in locations close to the release sites. The maximum distance between the capture and recapture positions was ≈300 m, and the time between recaptures ranged between 7 and 185 d (Table 5.2).

Table 5.1 The number of *Diplodus annularis* tagged with standard T-tags and recaptured for each length interval.

Length interval (cm TL)	Tagged	Recaptured
8-10	12	0
10-12	266	0
12-14	686	13
14-16	175	2
>16	10	0

Table 5.2 The number of recaptured *Diplodus annularis* according to the distance from the tagging position and time between recaptures

	<100 m	100-500 m	>500 m
<1 week		2	
1-2 weeks	8		
2 weeks to 1 month	1		
1-3 months	2		
>3 months		2	

5.3.2 Acoustic telemetry

The 2008 acoustic receiver array was able to detect all tagged fish (n = 12), whereas two (25%) fish tagged with acoustic transmitters in 2009 (n = 8) were not detected. Fish detections are summarised in Table 5.3. The movement patterns of *D. annularis* detected using acoustic telemetry were very different for displaced and non-displaced individuals. While displaced individuals were detected by several receivers for few hours and then get out of the acoustic array, most of the non-displaced individuals were detected by only one receiver and remained within its coverage for a longer period (Table 5.3). Two fish (#11 and #D3) were not detected by any receiver, and we also considered not taking into account fish #D1 as only four detections were recorded by only one receiver. In addition, fish #D7 and #D9 were continuously detected by only one receiver during consecutive days (up to 31 and 29 d respectively), which could suggest that they had either lost their tag or died (e.g., Taylor et al., 2006; Abecasis et al., 2009). In contrast, fish #D8 was also only detected by one receiver, but for this fish the detection pattern was intermittent, which suggests that it often moved out of the range of the receivers. The detection patterns for fish #D5 and #D11 were also intermittent, but these fish were detected by more than one receiver. However, these receivers were located close to each other, which suggests that fish #D5 and #D11 moved within a reduced area.

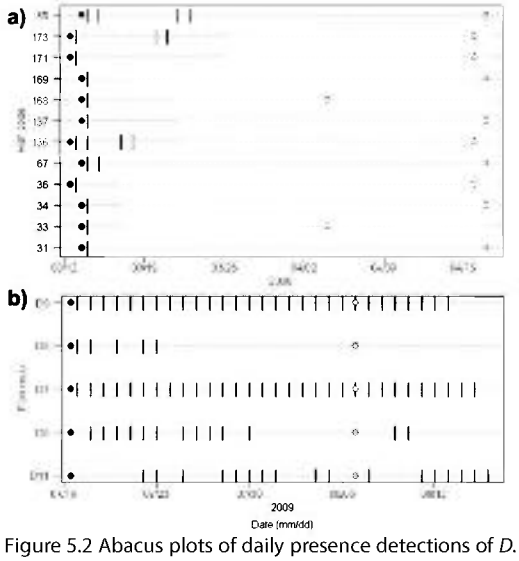

Figure 5.2 Abacus plots of daily presence detections of *D. annularis*. Vertical lines indicate the dates on which tagged individuals were detected within the monitoring area during the 2008 (a) and 2009 (b) experiments. (•) Transmitter deployment dates; (○) predicted transmitter death dates.

Short-term residence differed among tagged fish (Figure 5.2). In the 2008 experiment, most of the displaced fish left the monitoring area one day or a few days post-release, and only some of them returned to the edges of the monitoring array after some days (Figure 5.2a). Fish were detected for total periods ranging between 1 and 9 d, with a mean of 2.8 d (Table 5.3). However, in the 2009 experiment, non-displaced fish remained within the monitoring area for longer

periods. Those fish were detected for total periods ranging between 1 and 27 d (with a mean of 15.5 d) (Table 5.3). Combining the R_I scores from the two experiments resulted in high values (0.90 ± 0.36, mean ± SD), which indicates that most of the fish remained continuously within the monitoring area during the monitoring period. However, some fish (i.e., fish #173, #185 and #D5) exhibited an intermittent daily pattern throughout the monitoring period.

Table 5.3 Summary of the monitoring data for the 21 tagged *D. annularis* individuals. TL, total length; TP, total time period between the first and last date of detection; DD, number of days detected; and R_I, residence index. No R_I value for fish #D1 is presented as only a few detections occurred.

Fish code	TL (mm)	Weight (g)	Release date (yy/mm/dd)	First date of detection (yy/mm/dd)	TP (d)	DD (d)	R_I	Total detections	No. of receivers
36[a]	141	44	08/03/13	08/03/13	1	1	1.00	13	4
185[a]	141	48	08/03/14	08/03/14	9	4	0.44	78	8
168	142	48	08/03/14	08/03/14	1	1	1.00	27	5
171[a]	143	46	08/03/13	08/03/13	1	1	1.00	16	5
33	143	46	08/03/14	08/03/14	1	1	1.00	18	3
137[a]	143	48	08/03/14	08/03/14	1	1	1.00	70	5
169[a]	144	51	08/03/14	08/03/14	1	1	1.00	23	4
173[a]	145	53	08/03/13	08/03/13	9	3	0.33	138	6
67[a]	152	56	08/03/14	08/03/14	2	2	1.00	103	5
34[a]	153	58	08/03/14	08/03/14	1	1	1.00	10	4
31[a]	154	64	08/03/14	08/03/14	1	1	1.00	34	6
136[a]	157	58	08/03/13	08/03/13	6	4	0.67	41	3
D1	148	59	09/07/17	09/07/28	2	2	-	4	1
D8	148	58	09/07/17	09/07/17	7	5	0.71	25	1
D11	152	64	09/07/17	09/07/22	27	17	0.63	82	2
D7	153	65	09/07/17	09/07/17	31	31	1.00	651	1
D9	153	65	09/07/17	09/07/17	29	29	1.00	437	1
D5	165	82	09/07/17	09/07/18	26	13	0.50	128	3
11[a]	152	63	09/07/17	-	-	-	-	0	0
D3	148	58	09/07/17	-	-	-	-	0	0

[a] Fish tagged with transmitters that were programmed to run intermittently to yield an active period of 12 h d^{-1}

5.3.3 Displacement experiment

Eight individuals (67%) from the displaced fish showed evidence of directional movement towards the capture location (Table 5.4 and Figure 5.3). The time taken to return to the capture site ranged between 0.75 h and 15.25 h (4.66 ± 4.64, mean ± SD). High LI values (0.75 ± 0.19, mean ± SD) in most of the fish indicated that movement from the release site to the capture location tended to be unidirectional (Table 5.4). Capture locations were located at the margin of the acoustic array. After fish returned to the vicinities of the capture site, most of them were no longer detected by any receiver. However, two individuals (#173 and #185) were intermittently detected some days after having returned to the capture site by the receivers located in the same vicinity.

Table 5.4 Summary of tagging and return (homing) conditions for individuals of *D. annularis* released ≈1500 m from the capture location. Distance travelled to return and the linearity index are based on COA locations.

Fish code	Time taken to return (h)	Distance travelled to return (m)	Linearity index
36[a]	1.25	1328	0.818
185[a]	15.25	1929	0.568
168	2.5	1505	0.757
171[a]	6.5	1555	0.908
33	-	-	-
137[a]	4.25	2074	0.536
169[a]	-	-	-
173[a]	3.75	706	0.952
67[a]	-	-	-
34[a]	0.75	1001	0.972
31[a]	3	2162	0.512
136[a]	-	-	-

[a] Fish tagged with transmitters that were programmed to run intermittently to yield an active period of 12 h d^{-1}

5.4 Discussion

Despite the effort made to inform the fishing community and the rewards offered for recaptures (Cardona-Pons et al. 2010), only 11 individuals *D. annularis* were recaptured by recreational anglers. Tag shedding could be one of the main factors explaining such a low recapture rate. Other factors, previously mentioned in Abecasis et al. (2009), that could lead to low recapture rates are that: (1) anglers avoid declaring tagged fish below the minimum legal landing size of *D. annularis* (12 cm); and (2) tagging could increase vulnerability to predators (colonisation of external tags by algae was frequent in our study). All these factors could be responsible for reducing the probabilities of recapturing tagged fish. However, inferences of movement rates that are not biased by tag loss effects (i.e. tag shedding, non-reporting rate and tag-induced mortality) can be determined by recapture-conditioned estimators based on only-recapture data (McGarvey 2009). The lower rate of tag recapture (1.31%) was close to other similar studies. Based on an extended dataset (i.e. wider area, longer period and more tagged fish), the recapture rate of *D. annularis* in southern Mallorca was 0.7% (Cardona-Pons et al. 2010). In addition, the same study also reported similar recapture rates for *Coris julis* (4.6%) and *S. scriba* (0.8%), which are two of the most targeted species by the recreational fishery. In a previous study conducted with other species of the same genus, (Abecasis et al. 2009) reported recapture rates of 3.13% for *Diplodus vulgaris*, and 4.08% for *Diplodus sargus*.

The information obtained from the external tags suggests that *D. annularis* does perform small displacements. Distance between mark and recapture may be biased when fishing effort and/or release locations are clustered. For example, releasing all fish near a location with high concentration of fishing effort could cause underestimation of distances between release and recapture. In our study, tagging locations could be considered as randomly distributed within the suitable habitat for *D. annularis* (Figure 5.1, lower inset). In addition, although recreational fishing effort cannot be considered strictly homogeneous (Chapter 7), its current spatial variation in Palma Bay is not enough large to induce a severe bias in the

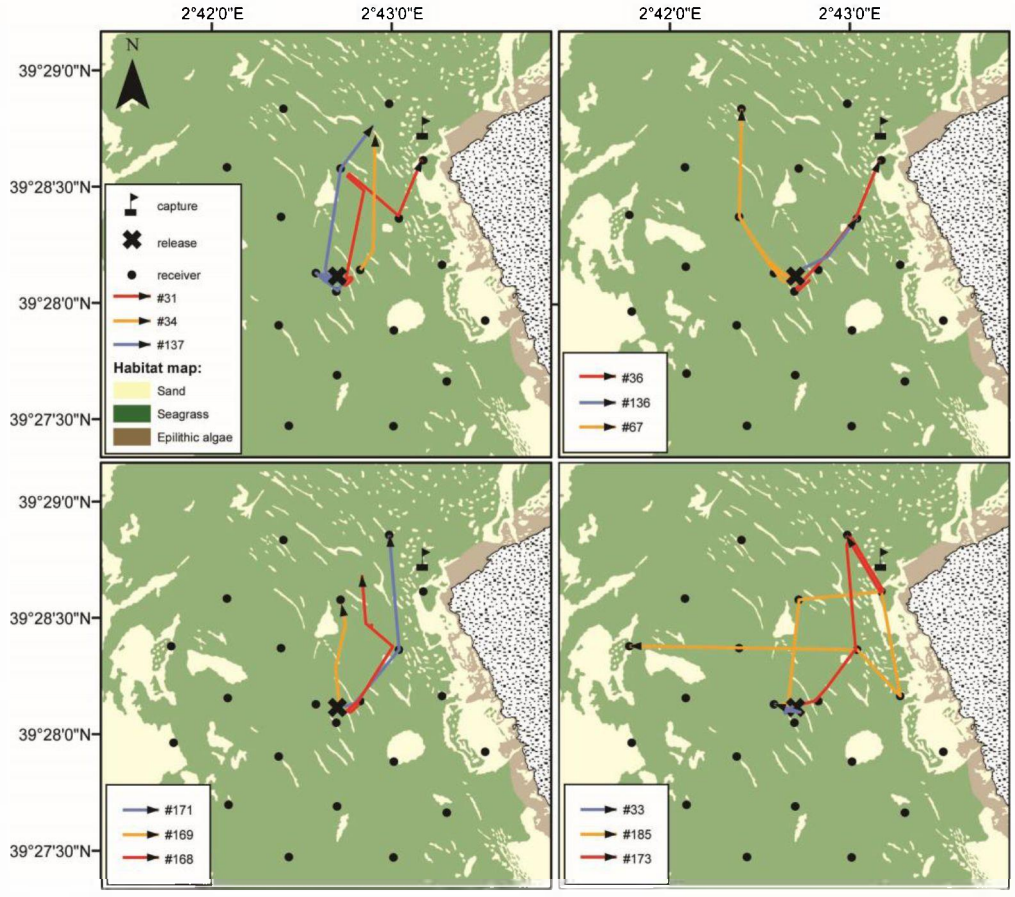

Figure 5.3 Paths representing the movement patterns of the 12 displaced individuals of *Diplodus annularis*. Paths are based on COA locations and do not represent true locations.

estimated distances (Palmer et al. 2011). Unlike acoustic data, which are limited due to the battery life of transmitters, fish recaptures can provide information for a time span over 1 month. In our case, the four fish that were recaptured after 1 month and within maximum distance of ≈300 m provides valuable information to assess the high site fidelity of this species.

Acoustic telemetry data complemented conventional tagging by providing new information on the short-term movements of *D. annularis*. However, as in other studies, the low number of tagged individuals by acoustic tags represents a limitation (Abecasis and Erzini 2008, Abecasis et al. 2009). In addition, a common problem when working with small fish is the difficulty in capturing individuals large enough to be fitted with acoustic transmitters. In our case, this factor was especially relevant in the displacement experiment: after receiver deployment there was a lack of availability of fish with an adequate size in the study area. This fact compromised the experimental design and we were unable to capture fish in locations with a better coverage of receivers (i.e., not so close to the edge). It compromised the capability of the monitoring system to detect whether fish presented a homing behaviour, as most of the fish were no

longer detected once they had pass through to the capture site. Even if fish would have established their home range close to the capture location (e.g., Kaunda-Arara and Rose 2004), such pattern could not be easily detected by the receivers, as the capture location was close to the edge of the acoustic array. Nevertheless, despite of these limitations, we consider some direct and indirect evidences that could be consistent with a homing behaviour: 1) directional navigation movement towards the capture location was not random (8 from 12 displaced fish); 2) one individual (#173) was detected intermittently by the receivers near to the capture location; 3) results of conventional tagging and non-displaced fish in 2009 (i.e., they could be considered as a control group) suggest a high site fidelity behaviour that has been related previously with homing abilities (e.g., Kaunda-Arara and Rose 2004); and 4) homing abilities have been documented in other species of the Sparidae family, such as *Sarpa salpa* (Jadot et al. 2006) and *Sparus aurata* (Abecasis and Erzini 2008). Spatial learning through different homing mechanisms (i.e., cognitive mapping, social transmission and landmark orientation) may allow fish to navigate back to resting, foraging or spawning sites (Kaunda-Arara and Rose 2004).

The information derived from the acoustic array deployed in 2009 contrasts with the data obtained from the 2008 array. The performance of the acoustic array in this study is relevant. The separation between receivers produced areas of non-continuous detection. This fact compromised the capability of the system to discriminate between fish with a reduced home range (i.e., less than the distance between receivers) and fish that could have been dead or lost their tags. In Chapter 4 we determined that the detection of additional patterns (e.g. diel periodicities in the number of detections) could suggest that fish could be alive when detected by only one receiver. However, that was not the case for fish #D7 and #D9 and we did not consider them for analysis. Moreover, due to fish availability, the release locations were in shallow waters (<10 m) where the detection range may be greatly reduced due to signal absorption and background noise. Fish that were not displaced were rarely detected by different receivers. Although the spacing between receivers was higher than the array deployed in 2008, these results would suggest a high site fidelity. This pattern is consistent with the results reported by conventional tagging. In addition, similar results were reported for individuals of *Diplodus vulgaris*, where fish were detected by only one receiver during long periods of time (Abecasis et al. 2009).

The results of this study provide valuable information for the management of recreational fisheries and MPAs. *D. annularis* has been used in recent studies to evaluate the direct and indirect effects of the recreational fishery in the Balearic Islands (Cardona et al. 2007, Alós et al. 2008, Alos et al. 2009, Cerdà et al. 2010). The importance of site fidelity relies on the exposure of this species to the local environment over time. Some evidence can be extrapolated from a previous study in which *D. annularis* showed differences in diet between artificial reef and control habitats in *P. oceanica* meadows, in which blocks were deployed in an area of similar size to our acoustic arrays (Sánchez-Jerez et al. 2002). Thus, if *D. annularis* shows high site fidelity, it could be a good bioindicator for assessing local exposure to environmental factors (e.g., fishing overexploitation). Our results provide different information sources that could be used to complement each other in MPA management. Within MPAs site fidelity may enhance the likelihood of sustaining locally reproducing adults that could provide sources of dispersing larval recruits to adjacent fishing grounds (Kaunda-Arara and Rose 2004). The evidence of high site-fidelity in the present work indicates that MPAs could play a vital role in conserving these fish and managing the recreational fishery.

Acknowledgements

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SECTION IV. RECREATIONAL FISHERY

Chapter 6
Modeling fishing quality

ABSTRACT:

Increasing effort to analyze the spatial and human dimensions of anglers is necessary to improve fisheries management. Fishing quality is considered to be one of the most important variables afecting angler site choice. This Chapter provides a geospatial framework for assessing and mapping fishing quality in recreational fisheries. The framework relies on three main components: 1) experimental angling records for calculating fishing quality metrics, 2) spatial modeling for making predictions at unsampled locations, and 3) angler preference information for generating an integrated fishing quality index. We calculated different fishing quality metrics (i.e., catch per unit effort, yield per unit effort, mean fish size, price per unit effort, fish diversity) using fishery-independent experimental surveys. We then used regression models (Generalized Linear Mixed Models) to predict and map these metrics based on environmental and angler-related variables. Lastly, we combined Geographic Information System (GIS) and Multi-criteria Analysis (MCA) to integrate all metrics into a single index, considering alternative consumptive orientation profiles (i.e.,, generic, consumptive and trophy anglers). Our results demonstrate that spatially explicit environmental variables (i.e., slope, bathymetry, benthic habitat and coastal protection) can predict the spatial distribution of fishing quality metrics. In addition, we found a significant effect of a marine protected area (MPA) on price, providing insight into the role of partial protection for recreational fisheries management. Mapping and modeling fishing quality will increase our understanding of angler site choice and the factors underlying spatial patterns in the fishing effort and harvest (Chapter 7). The geospatial framework presented here can be used to inform ecosystem-based fisheries management.

6.1 Introduction

A greater understanding of the processes governing angler site choice can provide new insights into the spatial distribution of recreational fishing effort. In contrast to commercial fishermen who tend to focus on optimizing economic gains, recreational anglers have a more complex suite of motivations (Johnston et al. 2010). Hunt (2005) proposed that six general attributes affect a recreational fisher's site selection, maximizing personal utility: cost, fishing quality, environmental quality, facility development, encounters with other anglers, and regulations. Fishing quality and catch-related variables play a major role in the site selections of anglers and fishermen in general (e.g., Spencer and Spangler 1992, Arlinghaus 2006a, Kyle et al. 2007). Although anglers are a heterogeneous group, the catch-related expectation is considered to be the primary criterion in an angler's choice of site and is of paramount importance to anglers (Matlock et al. 1988, Schramm et al. 2003, Arlinghaus 2006a).

The relative importance of fishery attributes varies widely among angler types (Kyle et al. 2007, Johnston et al. 2010, Johnston et al. 2013). Thus, the characterization of multiple fishing quality metrics can allow angler preferences to be incorporated into integrated fisheries-management models. The most commonly used metrics include catch rate standardized by effort (number of fish or biomass per unit of time, e.g., Schramm et al. 2003, Post et al. 2008, Hunt et al. 2011, Post and Parkinson 2012), fish size (Hunt 2005, Oh et al. 2005, Kyle et al. 2007), and fish diversity or preferred species (Finn and Loomis 2001, Smith et al. 2012). A major hurdle to assessing fishing quality is the nature and quality of the available data. Inference from interviews may be a solution (reviewed in Hunt 2005), although this method may be prone to bias (Steffe and Murphy 2010). Alternatively, model prediction using independent-fishery data (i.e., data obtained from research surveys or scientific stock assessment) and potentially explanatory variables may overcome this limitation (Heermann et al. 2013). Previous studies have focused on angler-related biotic and abiotic factors influencing fish catchability (Smith et al. 1993, Englin and Lambert 1995, Kuparinen et al. 2010, Heermann et al. 2013). Moreover, the indirect effects of management measures that enhance abundance should also be taken into account when assessing fishing quality. For example, spatial management measures such as marine protected areas (MPAs) can also affect fishing quality (Alós and Arlinghaus 2013). In addition, model prediction using spatial covariates could be used to predict fishing quality at unsampled locations with combination of Geographic Information Systems (GIS). However, studies addressing the spatial variability of fishing quality in recreational fisheries, particularly in open marine waters, are lacking.

In this Chapter, we provide a general framework for assessing the spatial distribution of fishing quality using a correlation approach. We calculate five fishing quality metrics (i.e., catch per unit effort, yield per unit effort, mean fish size, price per unit effort, fish diversity) and evaluate the predictive power of environmental and angler-related variables using a spatially explicit modeling approach. Then, we integrate the five fishing quality metrics into a single index based on three simulated scenarios of angler profiles. Alternative angler preferences to fishing quality metrics are evaluated in a spatially explicit manner through the combination of GIS and Multi-criteria Analysis (MCA). To the best of our knowledge, this is the first spatial approach to the assessment and mapping of fishing quality in marine recreational fisheries.

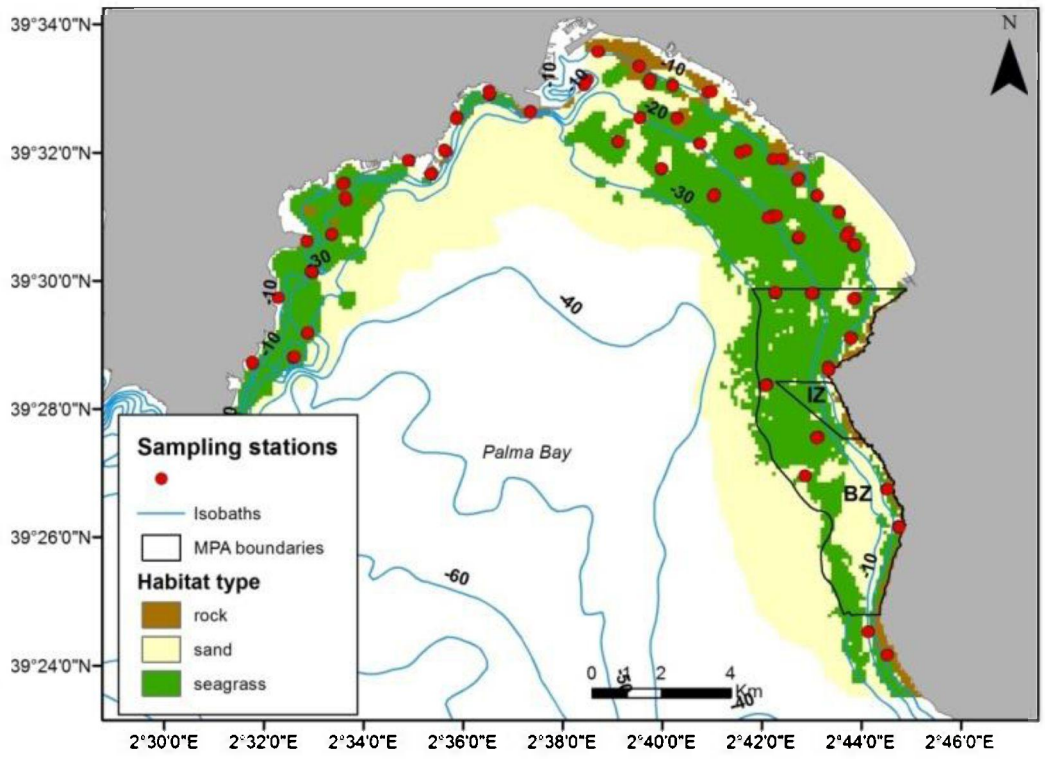

Figure 6.1 Study area and sampling locations with map of habitat type. MPA boundaries represent the Integral Zone (IZ) and the Buffer Zone (BZ).

6.2 Materials and methods

6.2.1 Experimental procedures

Independent scientific surveys were conducted over two campaigns (December 2006 to May 2007, and August 2007 to November 2007) at Palma Bay. Catch-related data were collected during boat-based experimental angling sessions. The sampling design included 49 randomly selected sites occurring over stratified depths and benthic habitats (Figure 6.1). Adjacent sites were separated at distances ranging from 421 to 1840 m. The experimental gear consisted of a hook and line with a rig composed of three identical hooks (size 12 large shank "J" hooks, Tubertini model 1T). We accounted for two angler-related factors: 1) bait type and 2) angler type. The bait was either a marine worm (*Perinereis aibuhitensis*) or a piece of shrimp (*Penaeus vannamei*), with bait pieces cut to similar sizes (Figure 6.2). Angler type was determined by years of fishing as in previous studies (e.g., Heermann et al. 2013): expert (≥ 10 years of fishing experience) and non-expert (< 10 years of fishing experience).

Each 30-min, anchored boat session was completed simultaneously by two anglers (yielding two angling sessions per site). The two anglers had different levels of expertise and used different bait types (e.g., expert, worm; non-expert, shrimp). Caught fish were identified to the species level, measured (total length to the nearest mm), and released. At the end of the 30 min angling session, the anglers moved to another

site and initiated a new session, using the alternate bait type. The time elapsed in moving between sites, changing the experimental gear, and anchoring the boat was excluded from the duration of the angling session. When all 49 sites were sampled, another full cycle of the same 49 sites was completed per campaign (i.e., two cycles in two campaigns). In the second cycle, bait type and angler type were reversed relative to the first cycle. With this design, each angler type completed four angling sessions at each site (i.e., two with worm; two with shrimp) for the two campaigns, yielding a total number of 392 sessions (i.e., two angler types, two cycles, two campaigns, 49 sites).

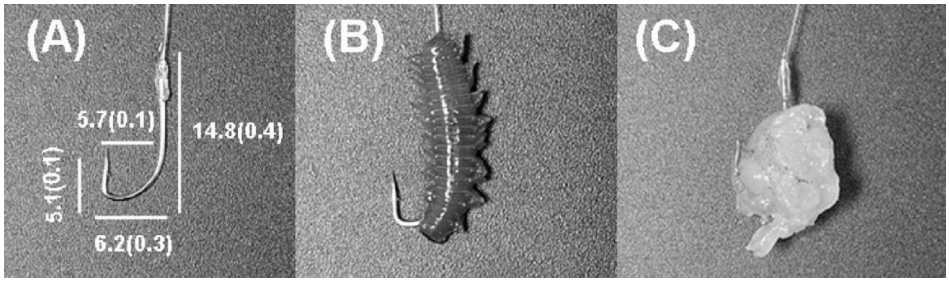

Figure 6.2 Hook dimensions (average ± S.E.; n = 5 hooks) in mm (panel A). Hook baited with marine worm (*Perinereis aibuhitensis*) (panel B) and hook baited with a piece of shrimp (*Penaeus vannamei*) (panel C). Reproduced from Alós et al. (2009).

6.2.2 Fishing quality metrics

We calculated 5 fishing quality metrics: 1) catch per unit effort (CPUE), 2) yield per unit effort (YPUE), 3) mean fish size, 4) price per unit effort (PPUE), and 5) fish diversity. CPUE was defined as the number of fish per 30-min session, pooling all species and including all samples (n = 392). YPUE was defined as the sum of weights per 30-min session, pooling all species and including all samples (n = 392). We estimated the weight of each fish using species-specific length-weight relationships presented in previous sources (Morey et al. 2003, Froese and Pauly 2010). Mean fish size was defined as the mean total length of all individuals per 30-min session, including only those samples where CPUE > 0 (n = 386). Estimates of PPUE took into account fish market price per species, as previous studies suggest that local anglers prefer high-value species (Morales-Nin et al. 2013). We calculated the PPUE (in euros, €), including all species, for each 30-min angling session (n = 392), applying the market price to each species. For each species we estimated the mean market price (i.e., € per kg) for the period 2009-2010 using the fish market database from the Government of the Balearic Islands. A number of low-valued species (n = 5, see Table 6.2) did not have a specific category and were usually sold within the same category of 'mixed-species' (locally known as 'morralla'). Finally, fish diversity was calculated with the Shannon index, accounting not only for the number of species but also the relative catch.

6.2.3 Predictor variables

We generated models of fishing quality metrics using putative explanatory variables selected as a priori. These variables included components of the spatial data of geomorphological models (depth and slope), benthic habitats, protection zoning, and temporal sea surface temperature data (SST). We used

GRASS 6.4.1 (Neteler et al. 2012) and the R package *raster* (Hijmans and van Etten 2010) to generate the maps at 100 x 100.

6.2.3.1 Geomorphological variables and benthic habitat

We used the digital bathymetric model (measured in meters, Figure 6.3A) and slope (measured in degrees, Figure 6.3B) maps developed in Chapter 3 (see Section 3.2.2.1 for details). Then, we generated a benthic habitat map of Palma Bay by combining the habitat type samples from Chapter 3 with the *Posidonia*-LIFE map from PBMR, already used in Chapter 2. We reclassified benthic maps into three categories (seagrass, sand and mixed rocky-seagrass), interpolated using Multilevel B-spline Approximation (MBA) algorithm (Lee et al. 1997), and rasterized them, up-scaled to the same resolution (i.e., 100 x 100 m cell size). The final map was used to define the study area for analysis (Figure 6.3C).

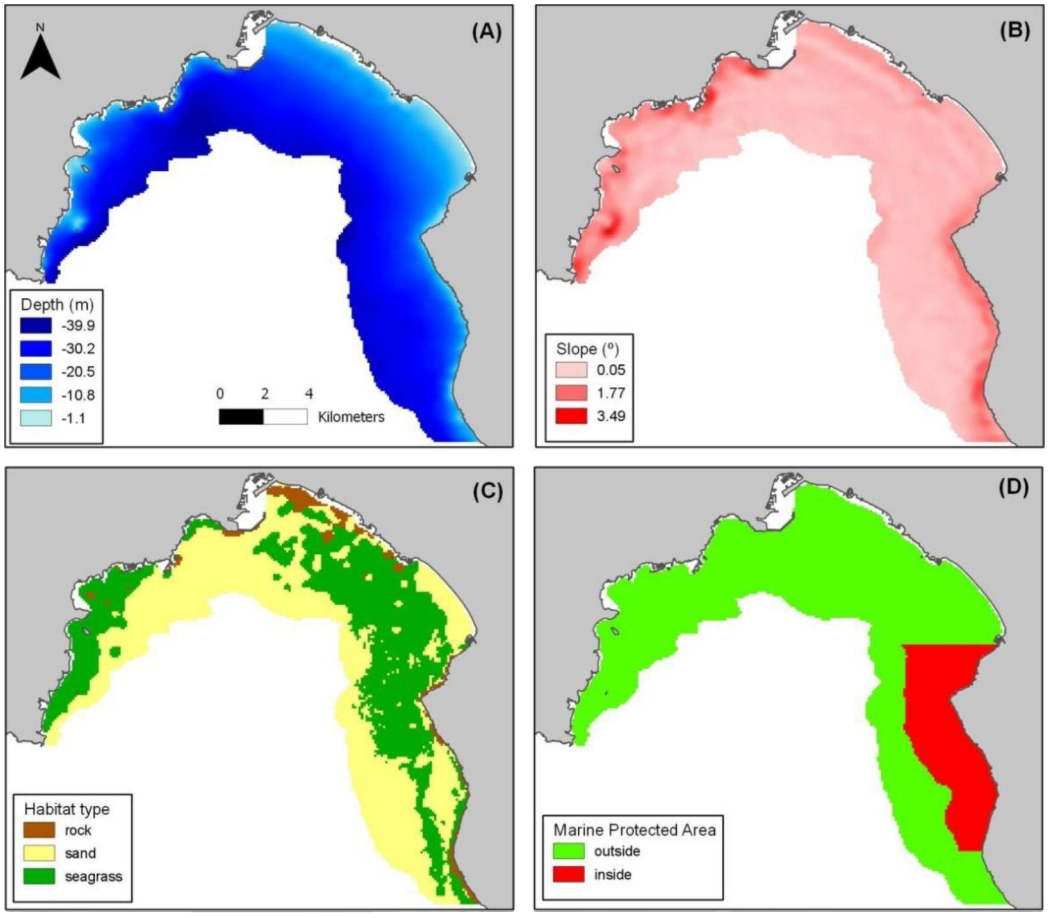

Figure 6.3 Maps of the predictor variables: a) bathymetry, b) slope, c) habitat, d) protection.

6.2.3.2 Protection zone

PBMR boundaries were considered as explanatory variable to assess the effect of protection. As no sampling locations were distributed within the Integral Zone, our categorical variable of protection zone had two levels: "inside" and "outside" of the partial MPA (pMPA, Figure 6.3D).

6.2.3.3 Sea surface temperature (SST)

We obtained a complete dataset of optimally interpolated satellite SST maps on a 1/16° resolution grid spanning the entire Mediterranean region over the 2006-2007 period from the MyOcean project (Buongiorno Nardelli et al. 2013). We extracted daily SST estimates for Palma Bay (39.45° N, 2.6°E), yielding values ranging between 13.8 and 26.0 °C throughout the study period and a mean of 18.9 °C (Figure 6.4).

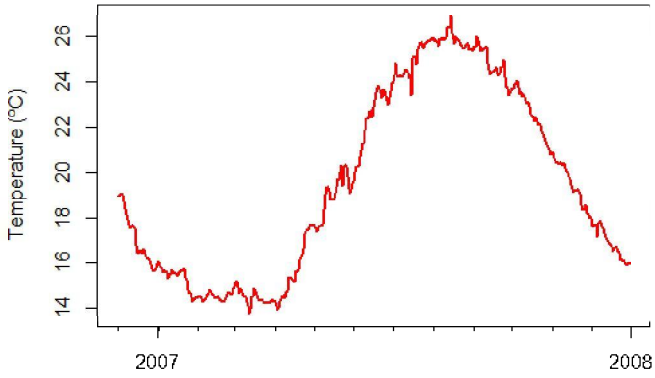

Figure 6.4 Temporal distribution of sea surface temperature (SST) in Palma Bay (39.45° N, 2.6°E) during the period of the study.

6.2.4 Spatial prediction

We used generalized mixed effect models (GLMMs) to analyze the effect of environmental variables on each fishing quality metric. We considered day of angling session (45 levels) and angling site (49 levels) as independent random effects and each environmental variable as a fixed effect. We also included two angler-related factors as fixed effects: years of fishing (expert vs. non-expert) and bait type (worm vs. shrimp). In addition, we added a quadratic form of depth to account for possible non-linear effects of bathymetry and incorporated the interaction of depth and SST to evaluate possible seasonal shifts along the bathymetric gradient.

We created a full model for each response variable (i.e., for each of the five fishing quality metrics) including all fixed and random effects (Bolker et al. 2009). We fitted all the full models with a GLMM using a Gaussian error distribution and estimated the parameters by restricted maximum likelihood (REML). We standardized the continuous explanatory variables (i.e., transforming them to yield a mean of zero and standard deviation of one) and checked for multicollinearity via the variance inflation factor (VIF). Homoscedasticity was examined through the visual evaluation of residual plots across categories and continuous predictors. We tested for normality by visually inspecting residual histograms, normal Q-Q plots, and the Shapiro-Wilk test. Where normality and homoscedasticity assumptions were violated, ap-

propriate transformations (e.g., logarithmic) were applied or outliers were removed. In addition, we calculated the semivariogram of the residuals for each model to check for the presence of spatial autocorrelation (SA, Legendre 1993); no SA was detected in any of the models. Model selection was then accomplished through information-theoretic procedures, starting from the most complex (i.e., full) model to the simplest (top-down strategy), using the Akaike information criterion (AIC). We first estimated the optimal structure of the random components and then proceeded with the fixed structure (Zuur 2009). Once the optimal model was obtained, we rechecked the assumptions of homoscedasticity, normality and SA. Pearson correlation coefficients were calculated to assess model fit. Model prediction for each response variable was conducted across the area defined by the presence of seagrass and rocky habitats (i.e., excluding sandy habitat) at a spatial scale of 100 x 100 m grid size. For illustrative purposes, we fixed the seawater temperature to 24.5 °C (the mean temperature during summer, corresponding to the period of major fishing activity as identified by Morales-Nin et al., 2005) and, where applicable, set angler bait to worm and angler expertise to non-expert.

6.2.5 Cumulative index and multi-criteria analysis

We quantified the cumulative preference of anglers to multiple fishing quality metrics while taking into account angler consumptive orientation profiles using GIS and multi-criteria analysis (MCA). We used the predicted maps of the five fishing quality metrics and assigned a weight to each to represent the relative preference from the angler's perspective. We used a weighted linear combination (Stelzenmüller et al. 2010) and quantified the relative cumulative fishing quality preference (CFq) for each grid cell (*i*) as

$$\mathrm{CFq_i} = \sum_{j=1}^{5} Fq_{ij} w_j \text{ and } \sum_{j=1}^{5} w_j = 1 \qquad \text{(Equation 6.1)}$$

where $\mathrm{CFq_i}$ is the cumulative fishing quality index at cell (*i*), Fq_{ij} is the value of fishing quality metric (*j*) at cell (*i*), *wj* is the weight assigned to the fishing quality metric (j). Because the five metrics were in different units, we log-transformed and normalized (rescaled between 0 and 1) the metrics following standard procedures (Halpern et al. 2008, Stelzenmüller et al. 2010). We illustrate this approach by generating three different scenarios: we defined three angler types (i.e., generic, consumptive, and trophy) based on three consumptive orientation profiles adapted from previous studies (Kyle et al. 2007, Johnston et al. 2010, Johnston et al. 2013). Generic anglers were assumed to be the least specialized and trophy anglers the most. With respect to the fishing quality metrics, generic anglers were assumed to (1) have an intermediate level of interest in CPUE, YPUE and PPUE, (2) have the least preference for average fish size, (3) be primarily interested in fish diversity, (4) use cheap bait (i.e., worm), and (5) be non-experts. Consumptive anglers were assumed to (1) be primarily interested in CPUE and YPUE, (2) have an intermediate level of interest in average fish size and PPUE, (3) have the least preference for fish diversity, (4) use a combination of worm and shrimp bait, and (5) have an intermediate level of expertise. Finally, trophy anglers were assumed to (1) be least interested in CPUE, YPUE and fish diversity, (2) be primarily interested in average fish size and PPUE, (3) use expensive bait (i.e., shrimp), and (4) have a high level of expertise. The simulated weights assigned to each fishing quality metric by the three angler types are presented in Table 6.1. We used the Pearson correlation coefficient to compare the three generated scenarios.

Table 6.1 Weights assigned to each consumptive orientation profile in calculating the cumulative fishing quality index.

Fishing quality metric	Generic	Consumptive	Trophy
CPUE	0.20	0.35	0.10
YPUE	0.20	0.35	0.10
Mean fish size	0.10	0.15	0.35
PPUE	0.20	0.15	0.30
Fish diversity	0.30	0.10	0.15
Sum	1	1	1

6.3 Results

6.3.1 CPUE

We sampled a total of 5,674 individual fish over 392 angling sessions, representing 29 species and 10 families (see Table 6.2). CPUE values ranged between 0 and 41 individual fish per angler per 30-min session, with a mean ± S.D of 14.5 ± 8.0. Slope alone was included in the optimal model as a spatial variable, revealing a positive relationship between CPUE distribution and slope (Figure 6.5A, Table 6.3). In addition, the selected model included temperature as a temporal variable (the higher the temperature, the higher the CPUE) and included both angling factors (with positive relationships between performance on both worm and expert anglers) (Table 6.3).

6.3.2 YPUE

The mean weights for each species are presented in Table 6.2. YPUE ranged from 0 to 1,257.2 g per angler per 30-min session and had an average ± S.D. of 373.7 ± 234.7 g. Depth was included in the final model with a positive parameter estimate, indicating that lower depths provided a higher yield (depth was included in the model with negative values). The predicted map (Figure 6.5B) illustrates this relationship across the study area. Temperature was included as a temporal variable, and angling factors exhibited similar patterns as CPUE (Table 6.3).

6.3.3 Mean fish size

Of all fish captured, the minimum size was recorded for an individual *Diplodus annularis* (4.9 cm) and the maximum for an individual *Labrus merula* (31 cm). The mean fish size per species is presented in Table 6.2. The mean fish size per angling session, considering all species, ranged between 7.4 cm and 18.1 cm, with a mean ± S.D of 12.7 ± 1.2 cm. Fish size was negatively correlated with slope and temperature. Habitat was also included in the optimal model, indicating larger fish sizes in rocky bottoms than in seagrass. Bait type was also a significant predictor, with larger fish caught using shrimp than worm. In addition, we found a significant effect of the interaction between depth and SST, indicating an increase in mean fish size from shallow water to deep water during summer, and the opposite pattern in winter. The predicted maps for summer and winter (Figure 6.5C and D) illustrate this relationship across the study area.

Table 6.2 Species and total catches during the experimental angling sessions. Average market price for each species between 2009 and 2010.

Species and family	Fish	TL (mm) (mean ± s.d.)	Weight (g) (mean ± s.d)	Market price (€ Kg^{-1}) (mean ± s.d)
Coris julis (Labridae)[a]	2472	129.6 ± 18.5	18.3 ± 8.2	2.33 ± 1.63
Diplodus annularis (Sparidae)	1705	115.4 ± 15.8	28.3 ± 12.7	1.03 ± 1.73
Serranus scriba (Serranidae)	601	132.6 ± 26.5	36.6 ± 23.7	7.78 ± 2.05
Diplodus vulgaris (Sparidae)	169	136.9 ± 31.9	45.4 ± 33.4	1.73 ± 0.96
Boops boops (Sparidae)	158	130.5 ± 22.0	19.8 ± 14.1	0.41 ± 0.27
Serranus cabrilla (Serranidae)	148	122.0 ± 21.2	21.6 ± 12.2	5.85 ± 20.87
Spondyliosoma cantharus (Sparidae)	127	125.0 ± 26.0	34.8 ± 26.1	4.01 ± 2.24
Pagellus erythrinus (Sparidae)	74	142.0 ± 35.3	41.8 ± 36.3	2.57 ± 1.59
Symphodus tinca (Labridae)	59	132.2 ± 48.2	42.3 ± 44.2	1.24 ± 0.96
Pagrus pagrus (Sparidae)	31	165.5 ± 34.6	81.3 ± 53.6	18.48 ± 6.43
Trachurus mediterraneus (Carangidae)	22	180.0 ± 46.2	46.7 ± 37.6	0.75 ± 0.96
Chromis chromis (Pomacentridae)[a]	20	103.3 ± 10.0	18.0 ± 4.9	2.33 ± 1.63
Trachurus trachurus (Carangidae)	20	145.0 ± 28.1	26.0 ± 14.2	0.75 ± 0.96
Symphodu socellatus (Labridae)	11	94.7 ± 12.7	10.8 ± 4.5	1.24 ± 0.96
Pagellus acarne (Sparidae)	8	101.3 ± 8.2	11.3 ± 3.0	0.95 ± 1.74
Serranus hepatus (Serranidae)[a]	8	65.4 ± 8.2	3.8 ± 1.7	2.33 ± 1.63
Oblada melanura (Sparidae)	7	136.1 ± 7.6	30.0 ± 4.8	1.28 ± 0.76
Spicara maena (Cetracanthidae)	6	103.0 ± 18.5	15.7 ± 10.2	0.48 ± 0.27
Labrus viridis (Labridae)	5	166.2 ± 74.2	83.7 ± 126.5	1.24 ± 0.96
Synodus saurus (Synodontidae)[a]	4	139.0 ± 69.2	33.1 ± 48.6	2.33 ± 1.63
Labrus merula (Labridae)	3	250.3 ± 56.8	243.5 ± 168.2	1.24 ± 0.96
Lithognathus mormyrus (Sparidae)	3	158.7 ± 60.7	58.5 ± 60.4	2.73 ± 1.62
Diplodus sargus (Sparidae)	3	157.7 ± 52.8	79.2 ± 57.2	2.07 ± 0.85
Sarpa salpa (Sparidae)	2	152.5 ± 29.0	52.7 ± 26.1	0.94 ± 0.68
Thalassoma pavo (Labridae)[a]	2	116.5 ± 0.7	19.1 ± 0.4	2.33 ± 1.63
Symphodus rostratus (Labridae)	2	99.0 ± 4.2	11.0 ± 1.5	1.24 ± 0.96
Mullus surmuletus (Mullidae)	2	173.0 ± 43.8	67.8	4.38 ± 1.86
Gobius niger (Gobiidae)[a]	1	112.0 ± n.a	15.4 ± n.a	2.33 ± 1.63
Trachinus draco (Trachynidae)	1	134.0 ± n.a	15.9 ± n.a	2.97 ± 2.00

[a] Species included in the low-value category of mixed-species.

6.3.4 PPUE

Fish market prices calculated for each species are presented in Table 6.2. The price ranged from 0.41 €/kg for *Boops boops* to 18.48 €/kg for *Pagrus pagrus*. PPUE ranged between 0 and 6.79 € per angler per 30-min session with an average ± S.D. of 1.12 ± 1.05 €. Slope and SST were positively correlated, and expert anglers performed better than non-experts. In addition, PPUE was the only variable for which a significant, positive effect of protection within the pMPA was identified by the model. The predicted map (Figure 6.5E) illustrates this relationship across the study area.

6.3.5 Fish diversity

The three most abundant species were *Coris julis*, *Serranus scriba* and *Diplodus annularis*. Two target species, *Pagrus pagrus* and *Labrus viridis*, were classified as endangered and vulnerable, respectively, by the IUCN Red List. The Shannon index was positively correlated with slope, SST, the quadratic form of

depth, and rocky bottoms. However, there were no significant effects of bait type or marine protection on fish diversity. The predicted map (Figure 6.5F) illustrates this relationship across the study area.

6.3.6 Cumulative fishing quality and consumptive orientation profiles

Maps of the cumulative fishing quality index according to the three simulated consumptive orientation profiles are presented in Figure 6.6A-C. The *generic* profile was highly correlated with both the *consumptive* ($r = 0.84$) and *trophy* profiles ($r = 0.88$); however, the correlation between the *consumptive* and the *trophy* profiles was lower ($r = 0.60$). Figure 6.6D shows the difference between the *trophy* and the *consumptive* profiles. Positive values represent locations that score higher for *trophy* anglers, whereas negative values represent locations that score higher for *consumptive* anglers. These results would suggest that anglers fitting to the *trophy* profile may be interested in fishing at deeper depths and within the pMPA, whereas anglers with preferences closer to the *consumptive* profile may prefer fishing grounds closer to shore and at shallower depths.

6.4 Discussion

We developed a geospatial approach to assess the spatial heterogeneity of fishing quality metrics, while accounting for a cumulative, multi-attribute utility function for recreational anglers. Using this approach, we have demonstrated that environmental and angler-related factors can be used to assess and map different fishing quality metrics. In addition, we propose that the combination of multiple fishing quality metrics into a single index is useful for accounting for different consumptive orientation profiles.

6.4.1 Spatial distribution of fishing quality

An understanding of how fishing quality is spatially distributed can allow future studies to test the hypothesis that angler site choice is determined by a catch-related variable or other factors. Studying the spatial distribution of fishing quality in the marine environment requires considering the spatial nature of environmental covariates and accounting for the potential confounding effects of spatial autocorrelation (Ciannelli et al. 2008). Exploration of our data revealed that spatial autocorrelation was not present in the residuals of our model, most likely due to the sampling design and the spacing among sampling sites.

This result is in agreement with a previous experiment that found no evidence of spatial autocorrelation between samples taken more than 75 m apart in ecosystems similar to the present study (Ordines et al. 2005). Once the spatial environmental covariates are incorporated in a model, then predictions at unsampled locations can be conducted within the domain space.

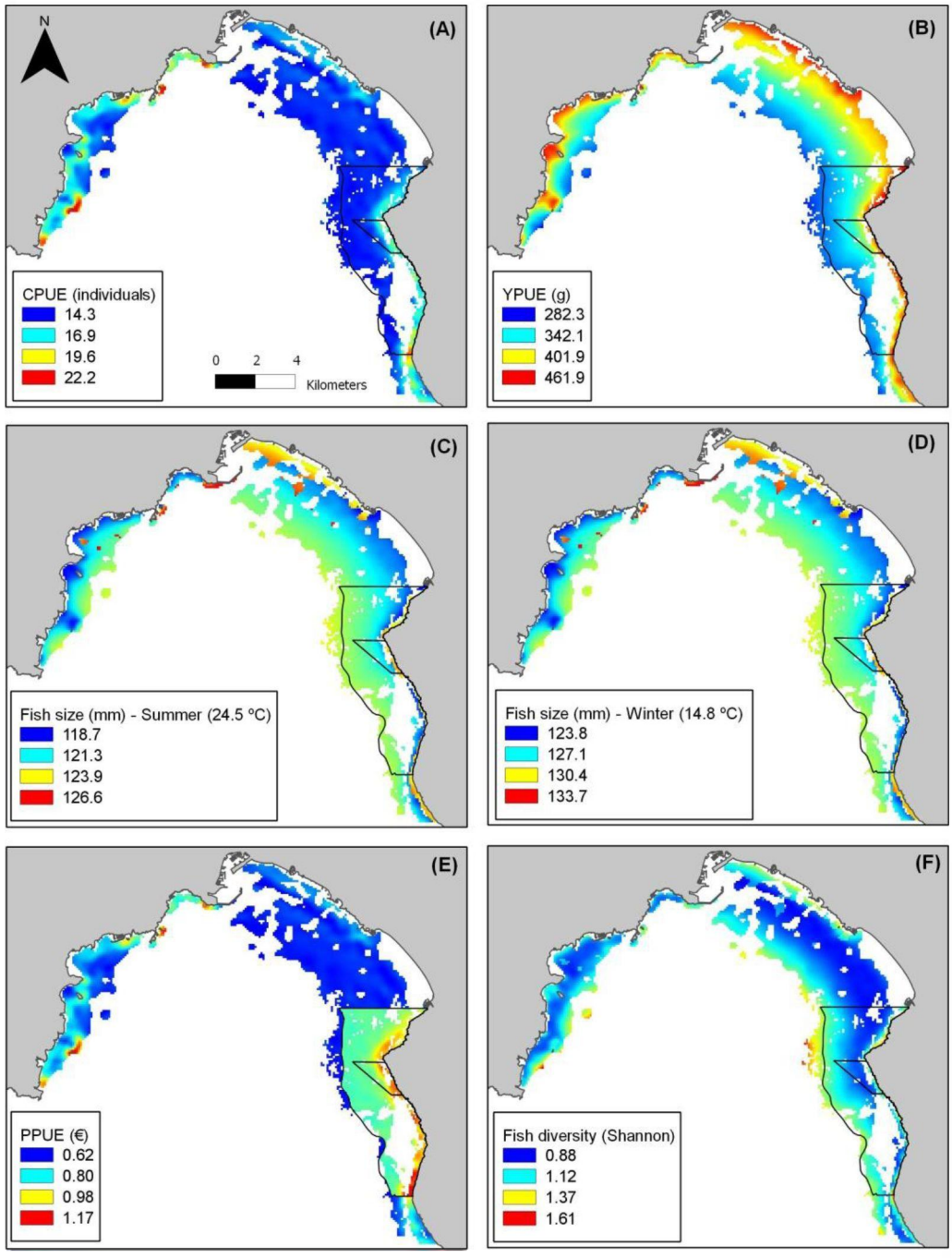

Figure 6.5 Predicted maps of five fishing quality metrics. For illustrative purposes, we fixed seawater temperature to 24.5 ºC and, where applicable, set bait to worm and angler expertise to non-expert. Predicted mean fish size is also provided for winter as the model identified a significant interaction between SST and depth. Solid lines represent MPA boundaries.

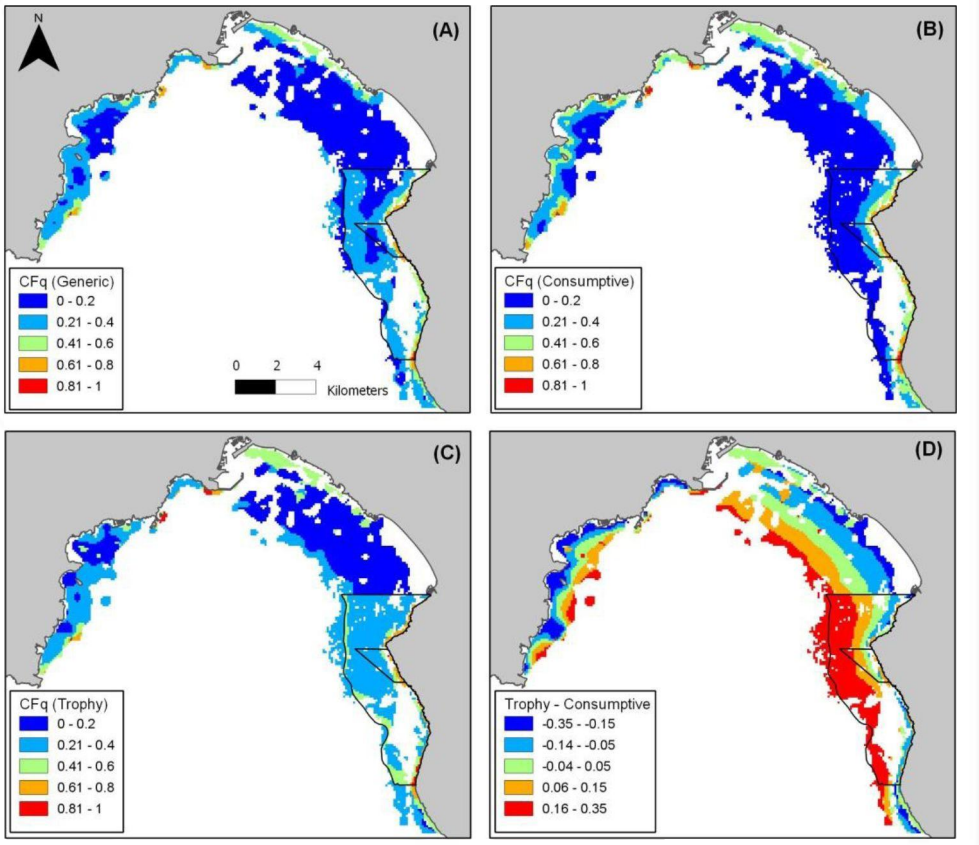

Figure 6.6 Cumulative fishing quality (CFq) index using GIS-MCA. A) generic anglers, b) consumptive anglers, c) trophy anglers, d) difference between trophy and consumptive anglers. Solid lines represent MPA boundaries.

6.4.2 Environmental effects

It is likely that catch rates vary in relation to the abundance of fish species and associated fish ecological conditions; however, CPUE can be an unreliable measure of fish abundance due to the selectivity of the gear and species size-dependent vulnerability (Harley et al. 2001, Stobart et al. 2012). The factors that can potentially affect fishing quality are diverse and may include a variety of ecological conditions (Heermann et al. 2013). Geomorphic metrics such as depth or slope may influence the distribution of fish species (Wedding and Friedlander 2008, Pittman et al. 2009). Our results identified that either slope or depth were significant predictors of all the fishing quality metrics investigated. Previous studies have not found clear relationships between fish density and depth within seagrass beds in littoral communities of the Mediterranean Sea (Fasola et al. 1997, Deudero et al. 2008). Areas of steep slope may indicate high topographic complexity, which could account for variation in abundance and richness (Pittman et al. 2009).

Table 6.3 Results of the generalized mixed effect models (GLMM) of the five fishing quality metrics. Estimates of fixed effects (S.E.) and significance are presented. The results correspond to the optimal models, with variable selection conducted using AIC.

Variable	CPUE	YPUE	Mean fish size[a]	PPUE[a]	Fish diversity
Intercept	18.84 (0.81)***	448.54 (23.05)***	4.858 (0.017)***	0.85 (0.07)***	0.85 (0.06)***
Slope	1.81 (0.60)**	-	-	0.09 (0.03) **	0.05 (0.02)*
Depth	-	35.47 (13.50)**	0.004 (0.007)	-	-
Depth^2	-	-	-	-	0.08 (0.02)***
SST	1.79 (0.55)**	47.12 (16.95)**	-0.020 (0.005)***	0.08 (0.02)***	0.16 (0.03)***
Depth * SST	-	-	-0.007(0.004)'	-	-
Habitat (seagrass)	-	-	-0.039 (0.019)*	-	-0.13(0.06)*
MPA (outside)	-	-	-	-0.16 (0.07)*	-
Bait (shrimp)	-3.70 (0.54)***	-43.41 (16.77)*	0.029 (0.007)***	-	-
Angler (non-expert)	-4.86 (0.54)***	-121.82 (16.79)***	-	-0.18 (0.03)***	-
Correlation (r)	0.797	0.729	0.718	0.705	0.601
Total observations	392	384	380	382	386

Significance codes: *** <0.001, ** <0.01, * <0.05, ' <0.1

[a] Response variables that were log-transformed.

Habitat type is an important factor affecting the spatial distribution of fish (Garcia-Charton et al. 2004, Crec'hriou et al. 2008). In our study, we found a significant effect of habitat type on mean fish size and fish diversity. We captured smaller-sized fish in seagrass beds than in mixed habitats. Regarding fish composition, previous studies have shown a high overlap of fish assemblages between seagrass and rocky bottoms (Guidetti 2000, Frau et al. 2003, La Mesa et al. 2011). Other authors have found that deeper seagrass contained more species and higher biomass than shallow seagrass, although depth effects were unclear (Deudero et al. 2008).

Seasonality (covarying with water temperature) is known to affect catch rate in several species (Margenau et al. 2003, Kuparinen et al. 2010). Our results are in agreement with previous studies conducted in *P. oceanica* meadows, where higher biomass, mean size and diversity values were found during the warmer summer months (Deudero et al. 2008, Kalogirou et al. 2010). This season corresponds to the recruitment peaks of some fish species, implying that a high number of juveniles became vulnerable to fishing during this time. We also found a significant effect of the interaction between depth and water temperature on mean fish size, with a greater abundance of smaller fish in shallow waters during the summer. This effect may also be related to spawning and recruitment patterns. Indeed, both habitat and depth effects can be the direct result of ontogenetic shifts in habitat selection, as described previously for coastal Mediterranean species (Macpherson 1998, Coll et al. 2013).

6.4.3 Angler-related factors

The heterogeneity of angler behaviour should be incorporated into integrated fisheries-management models (Johnston et al. 2010). In our study, we accounted for angler diversity with respect to two variables: 1) fishing practices, incorporating angler-related factors, such as angler experience and bait type, into the model; and 2) fishing preferences, accounting for consumptive orientation profiles.

Our results indicate that expert anglers perform better in terms of CPUE, YPUE and PPUE. Some previous studies have shown that angler skill affects catch rate (Arlinghaus and Mehner 2004, Heermann et al. 2013). However, others have found wide variation in individual fishing success, even among experienced anglers (Coll et al. 2004). The source of this variation is unclear (Morales-Nin et al. 2005). In the

present study region, angler experience may affect the efficiency of rod-and-line use and the time efficiency of fish release and re-baiting of the gear. Such efficiency enables greater catch rates and, hence, higher yield and fishing success. However, angler expertise did not affect average fish size or fish diversity. These results are in agreement with other studies demonstrating that anglers have less control over the size of fish captured than on the number (eg., Heermann et al. 2013). Nevertheless, we controlled for gear type in our experiment, with all fishers using identical gear. However, under natural conditions, expert anglers tend to use more specialized fishing gear to target larger fish, consistent with their profile as trophy anglers. In addition to angler experience, bait type also influenced some fishing quality metrics. The use of worm bait was associated with a higher number of fish caught and higher yield, although the average fish size was smaller than that obtained when fishing using shrimp. In contrast, there was no effect of bait on fish diversity or PPUE. Although bait type may have species-specific or size-dependent effects, our results, pooled across species, are in agreement with previous studies conducted in the same fishery (Alós et al. 2009). As both angler-related factors (bait and expertise) were included as independent factors in the model, the relative spatial pattern is the same for all combinations, and only absolute values may differ.

6.4.4 Coastal protection

MPAs have been identified as an effective tool for increasing the biomass and range of fish size spectra of exploited littoral fishes (Macpherson et al. 2002, Deudero et al. 2008, Coll et al. 2013). We found a significant effect of partial protection on PPUE. As PPUE is related to YPUE, and as this metric was unaffected by coastal protection, our results suggest that the pMPA acts to conserve the most valued fish species (assuming that most valued species are those with the highest market prices). This effect has been described previously for highly valued species (Coll et al. 2004). Although cause-and-effect is difficult to establish, the main effect of the pMPA of Palma Bay is attributed to the reduction in fishing effort (Alós and Arlinghaus 2013). In contrast, we found no significant effect of partial protection on the remaining metrics. These results conflict with those of previous studies in the same pMPA demonstrating positive effects on abundance, biomass and fish size (Alós and Arlinghaus 2013, Coll et al. 2013). However, these previous studies were conducted at the species-specific level, whereas the present study pooled all species together.

6.4.5 Limitations and extensions

Relative to studies in freshwater ecosystems, studies in open marine waters present two main challenges: 1) addressing mixed-species (rather than single-species) fisheries, and 2) accounting for greater fish mobility in open systems (relative to more restricted areas). In contrast to freshwater fisheries, where most case studies focus on one or few target species, we evaluated the mixed-species fisheries by pooling all species data, presenting a trade-off in complexity. Pooling all species allows us to capture a more realistic perception of anglers towards fish diversity. However, variation in abundance among species may cause different effects. For example, the distribution patterns of the most common species (i.e., *C. julis*, *D. annularis* and *S. scriba*) may have stronger effects than those of other, less abundant species. Nevertheless, we aimed to provide an overall measure of fishing quality, considering all species together. Such a measure is particularly relevant for a mixed-species fishery of over 30 different species. However, this approach

assumes that the spatial predictions of fishing quality metrics are stationary and unaffected by fish mobility. In our case study, the species composition of the overall catch was dominated by small-bodies species, such as *S. scriba*, *C. julis* and *D. annualis*, which have small home ranges and high site fidelity (see Table 6.4 for a summary of the movement studies on the species analysed in the present Chapter, including those studies presented in Chapter 4 and Chapter 5). Consequently, the fishing quality maps are likely robust enough to represent spatial heterogeneity.

Two main assumptions have been adopted in this work regarding angler preferences. The first one is related to species preference. Since recreational fishermen are not allowed to sell their captures, we used fish market prices as a proxy of the willingness to pay for a certain species. This assumption is supported by a recent study that found that recreational anglers prefer high-value species (Morales-Nin et al., 2013). However, we acknowledge that the results obtained for this metric should have to be taken with caution, specially the possible effect of the MPA. The second supposition depends on the weights assigned to the different angler consumptive orientation profiles. Although we used predefined weights based on a qualitative definition, our approach demonstrates that angler preferences should have to be taken into account in fisheries management. Thereby, we encourage further studies to conduct angler surveys for estimating multi-attribute preferences and integrate them with our geospatial approach.

Table 6.4 Summary of movement experiments conducted on fish species that are targeted by the 'roquer' fishery. Number of individuals (n), home range estimates (HR) and monitoring period correspond to acoustic methods only (i.e., passive tracling -PT-), except for the case of *Coris julis* where estimates are based on a numerical model using mark and recapture data (i.e. external tagging -ET-).

Species name	Region	Size (cm)	Methods	n	HR (km^2)	Period (d)	Reference
Coris julis	NW Mediterranean	11.7-16.8	ET	32	0.16	227	Palmer et al. (2011)
Diplodus annularis	NW Mediterranean	14.1-16.5	PT	20	-	27-185	This work (Chapter 5)
Diplodus sargus	NE Atlantic	19.3-26	PT	3	0.15-0.53[2]	1-62	Abecasis et al. (2009)
Diplodus sargus	NW Mediterranean	17-35	PT	74	-	22-269	Koeck et al. (2013)
Diplodus vulgaris	NW Mediterranean	24-27	PT	10	-	2-75	Alós et al. (2012b)
Diplodus vulgaris	Central Mediterranean	18.1-25.5	PT	12	0.002-0.09[1]	1-207	Mesa et al. (2013)
Diplodus vulgaris	NE Atlantic	18.8-21.5	PT	4	0.02-0.04[2]	1-260	Abecasis et al. (2009)
Sarpa salpa	NW Mediterranean	22.5-34	PT	20	0.88-1.87[3]	1-372	Pagès et al. (2013)
Sarpa salpa	NW Mediterranean	21.1-31.9	PT	18	0.002-0.279[3]	1-49	Jadot et al. (2006)
Sarpa salpa	NE Atlantic	28-35.2	PT	5	0.3-0.57[2]	1-296	Abecasis et al. (2012)
Serranus scriba	NW Mediterranean	16.9-21.7	PT	15	0.1-1.3[1]	1-36	This work (Chapter 4)
Serranus cabrilla	NW Mediterranean	12.2-17.4	PT	15	0.03-1.20[1]	4-61	Alós et al. (2010a)
Pagrus pagrus	N Atlantic	21-41	PT	22	0.06-2.7[1]	9-704	Afonso et al. (2009)

[1] HR estimates are based on combining utilization distributions (UD) and minimum convex polygon (MCP) methods; [2] HR estimates are based only on MCP; [3] HR estimates are based only on UD.

6.4.6 Management implications

Fishing quality information is relevant for the development of integrated fisheries-management models and can be used to inform optimal harvest regulation (eg. MPA design or minimum-size limit regulations). In addition, assessing fishing quality constitutes a first step towards an understanding of fishing effort patterns and can therefore contribute to the improved management of recreational fisheries (Chapter 7). Spatial allocation of fishing effort is important to the implementation of Marine Spatial

Planning (MSP) and Integrated Coastal Management (ICM) protocols, permitting consideration of interactions of recreational fishing with other human activities. The geospatial framework provided in the present study can be applied elsewhere, including freshwater or commercial fisheries, and may improve our understanding of fishermen behaviour in support of fisheries management.

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Chapter 7
Modeling fishing effort and harvest

ABSTRACT:

The main objective of this Chapter is to propose a general framework for predicting spatio-temporal patterns of fishing effort and fishing harvest in heterogeneous seascapes. First, angler's behaviour was modelled from a set of explanatory variables and using 188 boat allocation surveys. Boosted regression trees (BRT), a machine-learning method, was used to predict the number of boat outings at unsampled days and provide spatio-temporal estimates of fishing effort. Then, these estimates of fishing effort were combined with the estimates of fishing catch provided in Chapter 6. Uncertainty of the combined estimates was properly computed using bootstrap methods, which also take into account the number of fishers per boat and the duration of the fishing journey. The fishing effort for 2007 at Palma Bay was estimated in a total of 5,008 boat outings (range 95% CI: 4,031-6,221). More interestingly, the predictive model was able to capture the spatial heterogeneity (62.2% deviance explained, 0.8 correlation). The results obtained indicate that angler occurrence was mainly related to accessibility, weather conditions, and social factors like non-business days. Port-based accessibility was one of the major predictors of fishing effort, combined with wave height. Conversely, fishing quality metrics appeared to play a secondary role. These results suggest that the studied fishery is mainly driven by leisure motivations. Total harvest of a plausible scenario of angler expertise and bait type was estimated in 23.9 t per year (range 95% CI: 19.3-29.4). This figure would represent 27.6% of the total artisanal (commercial small scale boats) catch over the seagrass fish community, thus highlighting the relevance of this type of recreational fishing. This Chapter demonstrates the use statistical models to predict the spatio-temporal patterns of recreational fishers within complex socio-ecological systems. Such approach can be applied to any other human-prey system worldwide, including fishing or harvesting, and contributes to defining the basis of sustainable exploitation.

7.1 Introduction

Ecosystem-based management of nearshore marine resources depends on a deeply understanding of the spatial fine-scale patterns of exploitation (Crowder et al. 2008, Parnell et al. 2010). In fact, the spatial dimension of fisheries plays a key role on resource sustainability by determining the spatial structure of exploited fish populations and the spatial allocation of fishing effort (Lorenzen et al. 2010). Where fishers and their resources (i.e., fish) interact has, therefore, an evident implication for estimating fishing mortality and its uncertainty (i.e., two key aspects for stock assessment; Magnusson et al. 2013). However, the spatial dimension of fisheries is frequently ignored because it usually demands sophisticated social-ecological approaches and proper tools to obtain fine-scale data of the position of fish and anglers (Hunt et al. 2011, Fenichel et al. 2012, Post and Parkinson 2012). Because of that reason, a very limited number of studies have considered the spatial component of fishing mortality (Salas and Gaertner 2004). A better knowledge of spatial behavior of fish and fishers could notably improve our understanding of the fisheries dynamics and therefore improve the management of natural resources (Arlinghaus et al. 2013).

The spatial component of fisheries is especially relevant for estimating the total biomass harvested or the fishing mortality. Fishing harvest is a key parameter in population dynamics of exploited fish and is function of fishing effort and catch rates (Beverton and Holt 1957). Conventional population dynamics usually consider the fishing harvest as spatially homogeneous. However, it is well known that the distributions of the fishing effort and catch rates are highly structured (Bertrand et al. 2004, Bertrand et al. 2007, Poos and Rijnsdorp 2007). Many costal fish are linked to suitable habitats, and therefore is widely expected that catch rates will be spatially structured in function of the heterogeneity of the habitat. Because of that, the spatial structure of the catch rates, as well as the spatial allocation of the fishing effort, play a key role for estimating fishing harvest.

The allocation of the fishing effort include 'when to fish, where to fish, and what to fish' (Hilborn 1985). In order to better understand how fishers distribute on the space, fisheries are usually considered analogous to conventional predator-and-prey systems in which the human predators search for patches of preys (Post et al. 2008). Spatial explicit models are then appropriate for exploring fisher behavior (Pelletier and Mahevas 2005). However, the implementation of spatial-explicit approaches to fisheries has three major drawbacks: the complex nature of social-ecological systems, the lack of good quality monitoring data and the modeling approach (Cabanellas-Reboredo et al. 2014).

In contrast to commercial fishermen, who tend to focus on optimizing economic profits (Smith and Wilen 2003, Branch et al. 2006), recreational anglers have a more complex suite of motivations, generally referred as utility functions (Johnston et al. 2010). Different attributes at individual (i.e., angler) level can therefore determine the site choices in fisheries, including social (e.g. presence of other fishers), economical (e.g. travel cost) but also ecological factors (e.g. suitable habitat, catch rates) (Hunt 2005). Ignoring those attributes can lead to bias when using survey data to estimate fishing effort patterns (Hutton et al. 2004). Different works have explored how multiple factors may affect fishermen behaviour (see review van Putten et al. 2012). However, models usually rely of simple assumptions (Pelletier and Mahevas 2005), and less effort has been paid to integrate such factors using a quantitative approach (but see Dowling et al. 2013).

Beside the need for a social-ecological approach to the spatial dimension of fisheries, there is a general lack of reliable data. During last decades, commercial fishing activity has been monitored through electronic systems such as vessel monitoring systems (e.g., Murawski et al. 2005, Russo et al. 2014). In contrast, in recreational fisheries or in small-scale commercial fisheries, the acquisition of spatial data is challenging. The most frequent approach involves partial (i.e., samples of the spatial scenario and/or the temporal window considered) data on angler site allocation and harvest rates collected through different types of surveys and logbooks (Hunt et al. 2011, Post and Parkinson 2012). Despite some studies provided a descriptive approach (Lynch 2006, Stuart-Smith et al. 2008, Smallwood and Beckley 2012), different modeling methods (i.e., statistic or mechanistic) can be used to infer and extrapolate angler-effort patterns. Previous works implemented choice models, statistical models, or agent-based models (Dormann et al. 2012, Fenichel et al. 2012, Tidd et al. 2012). One of the main challenges that these methods have to deal with is the complex angler behaviour that determines the fishing site choice. Recent advances on modeling techniques such as numerical simulations (Patterson et al. 2001, Magnusson et al. 2013) or machine-learning tools provide new opportunities for addressing such challenges. For example, boosted regression trees (BRTs), a statistical machine-learning tool, is aimed to maximize both predictive capability and flexibility (Elith et al. 2008). BRT has been applied in fisheries research for analysing species distributions (Leathwick et al. 2006, Leathwick et al. 2008, Pittman and Brown 2011), assessing recreational angling catch rates (Heermann et al. 2013), modeling by-catch (Martínez-Rincón et al. 2012), and analysing fishing effort as well (Soykan et al. 2014).

The main objective of this Chapter is to propose a general framework for predicting spatio-temporal patterns of fishing effort and fishing harvest in heterogeneous seascapes. We combined recent studies on habitat and fishing quality mapping (Chapter 3 and Chapter 6, respectively), together with modeling techniques (Magnusson et al. 2013, Soykan et al. 2014). First, we modelled angler's behaviour with BRT using monitoring data (i.e., boat allocation from shipboard surveys) and a set of multiple explanatory variables. Second, we used the fitted BRT to predict the number of boat outings at unsampled days and provide spatio-temporal estimates of fishing effort. Finally, we combined the model of fishing effort with a previous model of fishing catch (Chapter 6) to estimate fishing harvest. In addition, quantitative estimates of model uncertainties were provided by bootstrap methods (Patterson et al. 2001, Magnusson et al. 2013).

7.2 Materials and methods

7.2.1 Modeling fishing effort

We used Boosted Regression Trees (BRT) to model the occurrence and density of angler boats at Palma Bay as a function of different predictor variables. BRT, also known as stochastic gradient boosting (De'Ath 2007, Elith et al. 2008), adaptively combine large numbers of relative simple tree models, to maximize predictive performance (Elith et al. 2008). BRT can handle categorical and continuous data, and allows dealing with missing data, collinear variables, non-linear responses and complex interactions among predictor variables. Further information is provided in the following subsections.

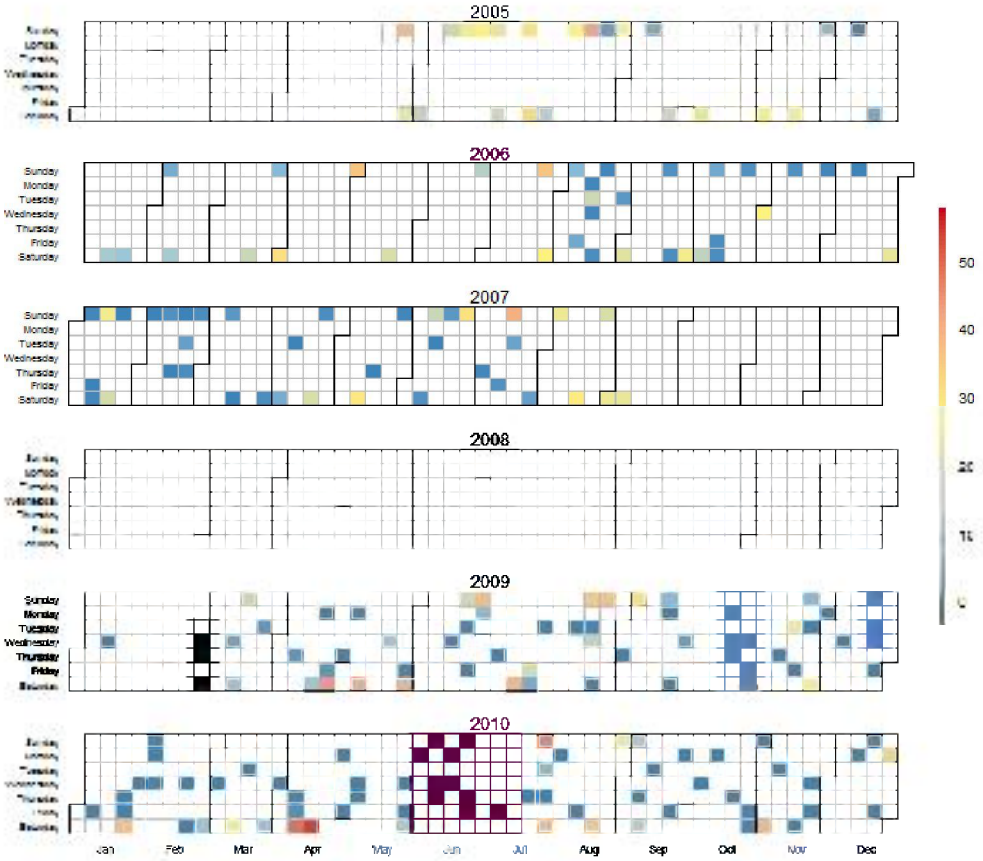


Figure 7.1 Calendar heat map of the observed number of boats per survey. Note that no surveys were carried out in 2008.

7.2.1.1 Data collection

We used the angling monitoring database (AMDB) generated by the Fish Ecology Group at IMEDEA. The angling monitoring program consisted on shipboard surveys (Lynch 2006, Dalton et al. 2010, Smallwood and Beckley 2012) across Palma Bay, where the positions of angling boats were georeferenced using a handheld GPS. On days where weather conditions restricted the use of the boat, observers confirmed the absence of anglers from different strategic land-based locations. The program began in 2005 and finished in 2010, with no surveys carried out during 2008. The spatial extent of each survey covered either a part or the entire bay, depending on logistic constrains and following a balanced sampling strategy. Temporal distribution of surveys followed a stratified random sampling, with higher monitoring effort allocated during weekends and morning periods based on previous results (Morales-Nin et al. 2005). A calendar map of the completed surveys is provided in Figure 7.1. Average time per survey was 120 min, with a total estimate of 480 h of observations. Recorded information in the surveys included information on the fishing modality, the number of anglers, the boat type and length, and the geographic coordinates together with the time of the sighting. For the present study, we selected those boats that were fishing using hook-and-line at depths lower than 35 m and over seagrass and rocky bot- tom (Figure 7.2a). In

addition, we selected those surveys that temporally overlapped with ≥ 65% of the boat anglers that practises the 'roquer' fishery (see Box 7.1 for details). As result, a total number of 188 surveys and 2,357 sampled boats were used in this study.

7.2.1.2 Explanatory variables

We identified different proxies for the factors that could influence the timing and locations of fishing trips by recreational fishers. We classified the predictors into three categories: temporal, spatial and spatio-temporal variables. Temporal variables included weather information, wave conditions and calendar data (e.g., business versus non-business days). Spatial variables included previous models of depth and habitat (i.e., those used in Chapter 6, see Figure 7.2b-c) plus a set of distance-based measures (e.g., distance to the coast, distance to natural areas). In particular, a gravity model was generated to represent the accessibility from ports, rather than the distance to the closest port (see Section 7.2.1.2.b for more details). Spatio-temporal variables consisted in protection zoning plus the fishing quality metrics generated in Chapter 6. Additional details for each variable can be found in the following subsections.

7.2.1.2.a Distance to the coast and natural areas

We calculated the distance to natural areas as a proxy for landscape aesthetics (Figure 7.2d). In order to differentiate between natural and artificial areas, shoreline units boundaries were used (Balaguer et al. 2008). For each grid cell we calculated the distance to the closest natural area, using the *gridDistance* function from the *raster* package. This function allows calculating distances at sea while taking into account a land mask. We used the same function for calculating the closest distance to the coast (Figure 7.2f).

7.2.1.2.b Port-based accessibility

The distance to the port is one of the usual measures used in commercial fisheries for explaining spatial distribution of fishing effort (Caddy and Carocci 1999). In most of the cases, the port of origin of a boat is known. In our case, the port origin for each boat was unknown, and in some areas of the bay there is a high density of ports. Thus, instead of calculating the distance to the closest access point for each cell (e.g., Stuart-Smith et al. 2008, Cabanellas-Reboredo et al. 2014), we proposed the use of a gravity model, similarly to previous approaches (Caddy and Carocci 1999). In our case, the potential accessibility to each cell is directly proportional to the number of moorings of each port (i.e.,, as a proxy of potential fishing power) and inversely proportional to the distance to each port. We obtained the number of mooring for each of the15 ports at Palma Bay (INESTUR-CIITIB 2007).

Then, for each cell (i) we calculated the distance the each port using the *gridDistance* function from the *raster* package. We then calculated and accessibility measure based on a gravity model:

$$PA_i = \sum_{h=1}^{15} \frac{M_h}{d_{ih}} \qquad \text{(Equation 7.1)}$$

where PA_i is the port accessibility index at cell i, M_h is the number of moorings of port (h), and d_{ih} is the distance between cell i and port h. We then rescaled from 0 (minimum accessibility) to 1 (maximum accessibility) using max-min rescaling: $[x_i - x_{min}]/[x_{max} - x_{min}]$ (see Figure 7.2d).

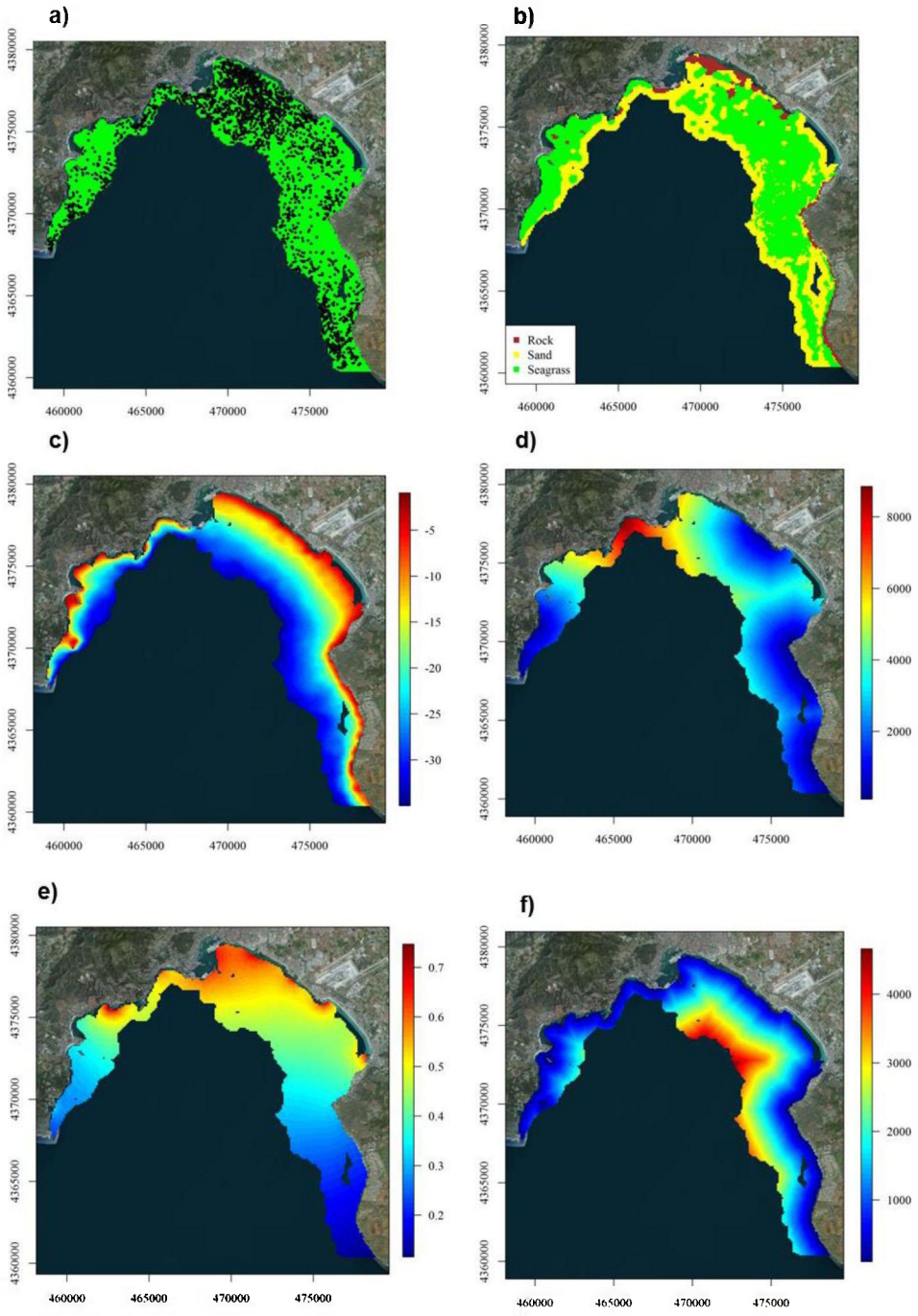


Figure 7.2 Study area and explanatory variables: a) the study area is represented in green, and was generated taken into account depths < 35 m and a buffer of 500 m from seagrass and rocky habitats. Black points represent all angler boats considered for analysis; b) benthic habitats; c) bathymetry (m); d) distance to natural areas (m); e) port-based accessibility; f) distance to the coast.

7.2.1.2.c Weather information

We obtained weather information from the National Meteorological Agency (AEMET, http://www.aemet.es) on a daily basis at Palma airport station (39°33'39"N 2°44'12"E, 8 m elevation). For this study, we used the following variables on a daily basis: mean, minimum and maximum air temperature (°C), precipitation (mm), solar hours and mean wind speed (m/s). Missing data was filled with information from either a neighbour station located at Palma harbour (39°33'12"N 2°44'12"E, 3 m elevation) or an external weather web service (i.e., http://www.wunderground.com/). Calendar maps of each variable can be found in Appendix C .

7.2.1.2.d Wave conditions

The wave conditions in the bay of Palma were characterized from the results of a wave model. For the period 2005-2009, the IMEDEA hindcast was used. It consists on a long-term simulation using the WAM model with a spatial resolution of 1/6° and forced by winds from the ARPEGE model (Jordà et al. 2012a), a dynamical downscalling of the ERA-interim reanalysis. An extensive validation of this hindcast can be found in Martínez-Asensio et al. (2013). For year 2010 the hindcast was not available and the results of the operational wave forecasts carried out by Puertos del Estado (WANA points; http://www.puertos.es/) were used. In this case the same wave model is forced by the regional wind forecasts carried out by the Spanish Meteorological Agency (www.aemet.es). In both models, 3-hourly time series of significant wave height (*Hs*, measured in meters) at the closest model grid point were used. For the surveys carried out in the morning we assigned the *Hs* at 9.00 am, whereas for the surveys that were conducted in the afternoon we used the *Hs* at 6.00 pm. Because of operational problems, the WANA model presented 7.6 % of missing data. This gap was filled with data from an oceanographic buoy at Palma Bay (http://www.socib.es). A calendar map of daily significant wave height can be found in Appendix C

7.2.1.2.e Calendar variables

For each survey we generated four variables based on the calendar date: month, year, business day and period of the day. We defined business days those from Monday to Friday, excluding public holidays. We obtained the national and local labour calendars from the Official Bulletin of the Balearic Islands (BOIB, http://www.caib.es/boib/). Business day was treated as two-factor variable. Period of the day was classified into 'morning' and 'afternoon'. We defined 'morning' as the period between sunrise and 12.00, whereas 'afternoon' as defined as the period between 12.00 and the sunset. A calendar map of business days can be found in Appendix C

7.2.1.2.f Fishing quality metrics

We predicted five fishing quality metrics (i.e., catch per unit effort, yield per unit effort, mean fish size, price per unit effort, fish diversity) using the models developed in Chapter 6. Spatial predictions depended on the maps of geomorphological variables (depth and slope), benthic habitat, and protection zoning that were available for the whole study area. Temporal variation was incorporated because sea surface temperature (SST) was found to be significant for the five metrics. A temporal series of optimal interpolated satellite SST at Palma Bay (39,45° N, 2.6°E) for the whole study period was obtained from the MyOcean project (see Section 6.2.3.3 for details). Predictions were carried out in the original 100 x 100 grid used in Chapter 6. Moreover, in order to take into account fish mobility, we calculated the focal mean of each

metric using the neighbouring cells that were located within 1 km. This distance is based on previous works that estimated the home range sizes of the most abundant species of this fishery (see Chapter 4, Chapter 5 and Table 6.4 for a summary of previous studies). Resulting maps can be found in Figure 7.3a-e.

7.2.1.2.g Protection zoning (MPA)

As mentioned in Chapter 1, PBMR is zoned into two management areas of differing levels of protection: (1) an Integral Zone (IZ, ≈2 km^2), where all fishing activities are prohibited; and (2) a Buffer Zone (BZ, ≈24 km^2), where artisanal fisheries are allowed under certain restrictions (e.g. limited access, gear restrictions) and recreational fisheries require a minimum hook size (7 mm gape), and fishing tournaments are banned. In addition, recreational fishing in the BZ is not allowed on Monday, Wednesday, and Thursday unless if they are holidays. The rest of the days, fishing is allowed and random coastguard controls are conducted. In this regards, we defined three levels of protection based on the permission and control: 1) *allowed*, corresponds to all the areas from Palma Bay that are outside the MPA, 2) *controlled*, corresponds to the BZ when fishing is allowed but additional inspections may be conducted by the guards of the reserve; and 3) *banned*, corresponds to the IZ, and the BZ when fishing is not allowed (Figure 7.3f). When defining the boundaries of the MPA we also accounted for a slight increase of the IZ declared in September 2006 (Official Bulletin of the Balearic Islands, Num. 128, Order num. 16162 of 1 September 2006).

7.2.1.3 Preprocessing

We calculated boat counts by intersecting boat positions with a regular grid. The grid had a spatial resolution of 1 x 1 km (projected in UTM zone 31N WGS84 datum) and covered the entire study area (i.e., 143 cells). Cell size was determined to account for fish mobility. Previous studies showed that most of the main target species presented home ranges within 1km^2 (see Table 6.4). In addition, a previous work identified that such grid resolution reduced the potential effect of spatial autocorrelation in model residuals (Cabanellas-Reboredo et al. 2014). Therefore, an observational unit for analysis was defined by the combination of each cell (i) and survey (v), resulting in a dataset of 24,527 units. For each observation unit, information of each explanatory variable was incorporated. Original datasets differed in their native resolution and were resampled following common geospatial methods. Continuous variables were resampled by calculating mean values, whereas for categorical variables covered surface of each category was calculated.

Although collinearity does not affect BRT predictions they can affect the interpretation of the model (Dormann et al. 2013, Soykan et al. 2014). We assessed collinearity among variables calculating the Spearman pair-wise correlation coefficient. Most of the predictors were uncorrelated (Spearman correlations < 0.7, Figure 7.4). Among those variables that were correlated, we selected *Tmax*, *Cpue* and *Seagrass*. The final list of 20 variables used in the analysis is presented in Table 7.1.

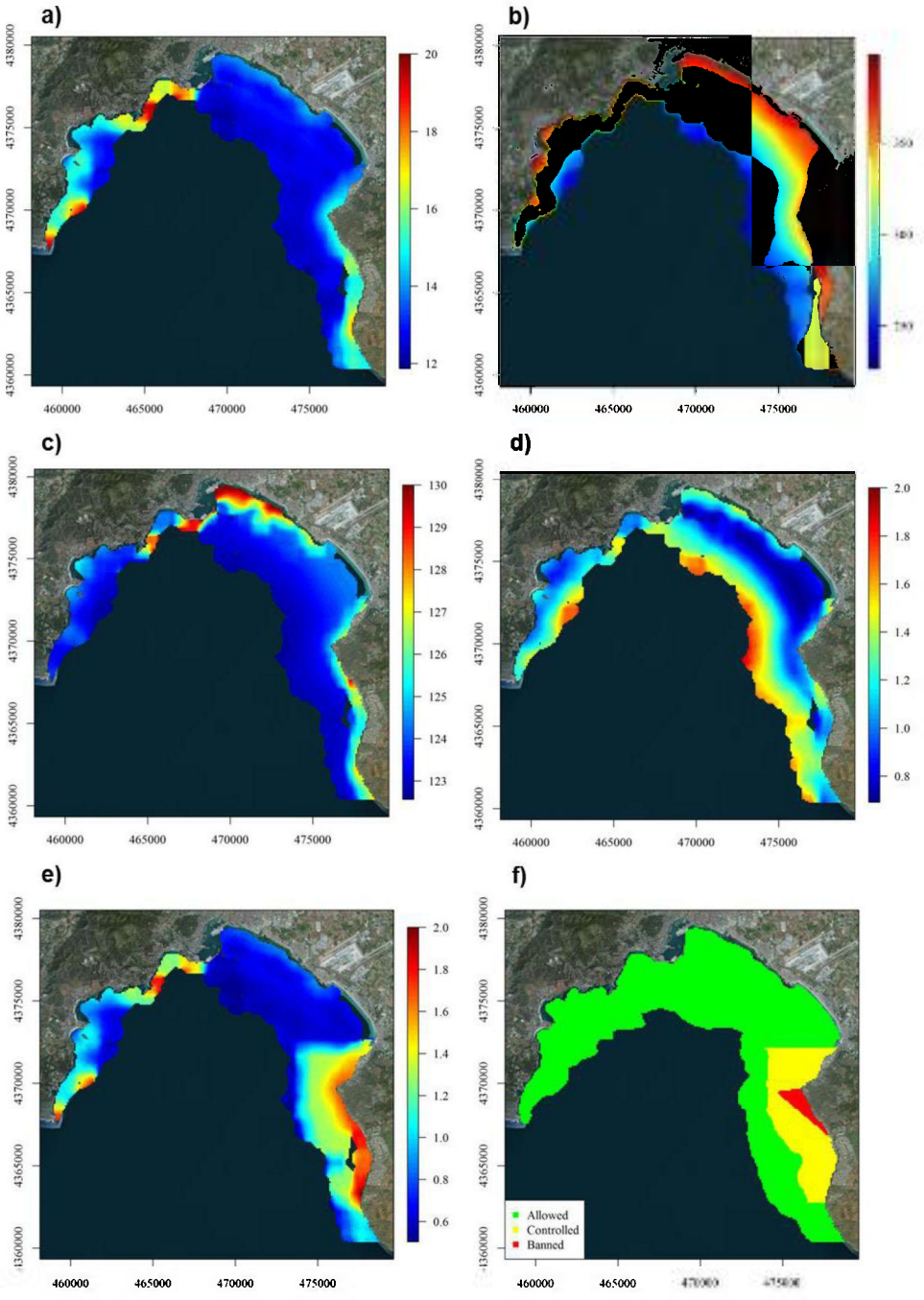


Figure 7.3 Spatio-temporal explanatory variables: a) CPUE (individuals per angler per 30-min session); b) YPUE (g per angler per 30-min session); c) mean fish size (mm); d) fish diversity (Shannon index); e) PPUE (€ per angler per 30-min session); f) protection zoning.

Before further analysis, the original dataset was partitioned into two sets: one set for model building with 70% of the data (a.k.a. training data set) consisting on 132 surveys and 15,643 observations; and the other set for model validation with 30% of the data (a.k.a. testing data set) consisting on 56 surveys and 6,581 observations. The partitioning was conducted per survey using a stratified random sampling that accounted for business day and day period (i.e.,, morning-afternoon) in order to reduce monitoring bias.

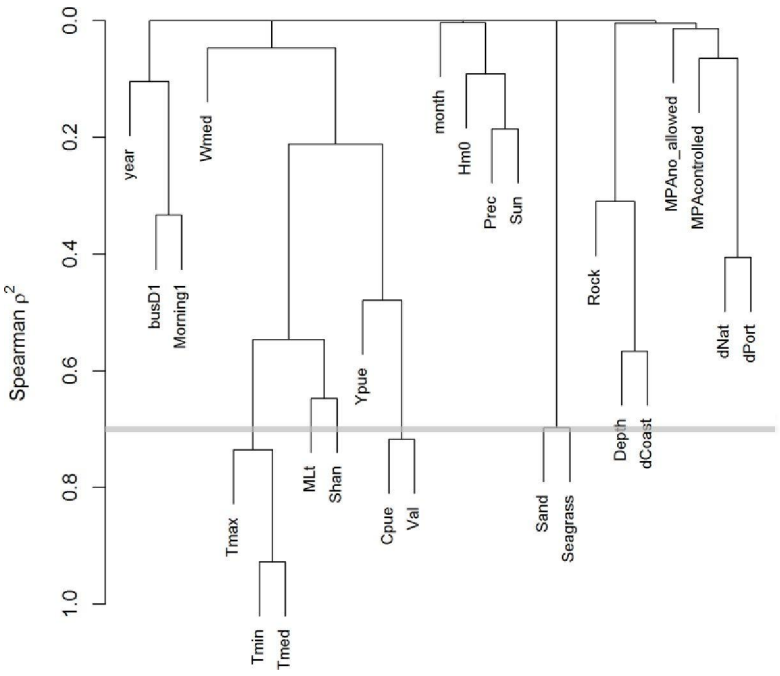


Figure 7.4 Hierarchical cluster on exploratory variables using squared Spearman correlation (ρ^2). The grey line represent $\rho^2 = 0.7$, a common threshold used for assessing collinearity (e.g., Dormann et al. 2013).

7.2.1.4 Model building

Given the highly skewed distribution of the boat count data (93.4% of the observations were zero), we fitted two BRT models assuming a hurdle model (Leathwick et al. 2008, Gregory et al. 2012, Oppel et al. 2012). The hurdle model consists of two parts. The first part used presence-absence data and predicted the probability of occurrence in each cell for each survey, assuming binomial distributed error. The second part used boat counts only (i.e.,, excluding all zeros) and predicted the number of boats per grid cell and survey, assuming Poisson distributed errors. Both models used the full range of predictors, allowing the identification of factors that influence presence and density separately. We also incorporated an offset term in the models aimed to account for spatial coverage (i.e.,, different monitored surface depending on the overlap of the cell with the study area) and temporal coverage (i.e.,, surveys conducted at time win-

dows with different chances to identify all boats in a day period; see Box 7.1 for details). Then, the offset was defined as:

$$Offset = log\ (sp_i) + log\ (temp_v) \quad \text{(Equation 7.2)}$$

where sp_i is the spatial coverage (in parts per unit) of cell (i), and $temp_v$ is the temporal coverage (in parts per unit) of survey (v). Finally, the predictions generated by the two models were then multiplied to provide an overall prediction of the density (i.e., number of boats per grid cell and survey) of angler boats.

BRT optimal parameters were estimated with an independent test set, using deviance reduction as the measure of success (Elith et al. 2008). BRT optimization is detailed in Box 7.2. Selected parameters for the binomial part were $tc = 5$, $lr = 0.005$, $bf = 0.6$ and $nt = 2350$ (see Table D1 in Appendix D); whereas for the Poisson part selected parameters were $tc = 5$, $lr = 0.001$, $bf = 0.7$ and $nt = 5250$ (see Table D2 in Appendix D).

BRT do not provide hypothesis tests to assess the significance (in the sense of frequentist, conventional tests do) of predictor variables, but the relative contribution (RC) of each predictor can be used as a proxy of its importance in defining the observed pattern. RC was determined based on how often the predictor is selected as a node within the BRT algorithm (Elith et al. 2008). RC of predictors were then scaled so that the sum adds up to 100%. In addition, partial dependence plots were generated to show the effect of a variable on the response, after accounting for the average effects of all other variables. These plots can be useful for interpretation of results, but they may not represent the effect of each variable in the same way conventional parametric model do. Interactions between predictors were explicitly modelled. However, although *tc* controls the maximum level of interactions, no information on the magnitude of the fitted interaction effects is provided. Therefore, interaction strength between pairs of variables was calculated (Elith et al. 2008). BRT were fitted using the *gbm* and *dismo* packages (Hijmans et al. 2012, Ridgeway and others 2013), plus custom code.

7.2.1.5 Model evaluation and calibration

We used the fitted BRTs to predict boat occurrence and density to both the training and testing data sets and assess their model performance (Potts and Elith 2006, Oppel et al. 2012). The percentage of deviance explained was calculated to provide an overall measure of the success of the fitting. Strong explanatory power is indicated by a high percent of deviance explained. For the binomial part we calculated the area under curve (AUC) as a discrimination performance criterion. For the hurdle model we calculated one measure of correlation, the Pearson's correlation coefficient (r) between the observed and predicted values, and one measure of error, the root-mean-squared error (RMSE). In order to evaluate the presence of spatial autocorrelation (SA) in the residuals (i.e., unexplained by the predictor variables), we calculated the Moran's I index per survey. Moran's I indicates the strength of the correlation between observations as a function of the distance that separates them. Its value ranges between 1 (i.e.,, strong positive SA) and -1 (i.e., strong negative SA), with zero indicate a random pattern (Fortin and Dale 2005). In addition, for the Hurdle model we also evaluated model performance at two aggregation levels (e.g., Cabanellas-Reboredo et al. 2014): 1) at the survey level (i.e., the sum of all boats observed per survey), and 2) at the grid cell level (i.e., the sum of all boats per grid cell throughout all surveys).

Box 7.1 Detection probability

We considered two different sources that can affect the probability of detecting boats in a given grid cell (*i*) at a given shipboard survey (*v*). The first source, a spatial component, relies on the approach used for counting the number of boats within a discrete grid of 1 x 1 km resolution. On the other hand, the second source, a temporal component, depends on the probability of detecting a boat angler given the time of the day. Such probability is a function of both the activity patterns of anglers, together with the timing of the surveys.

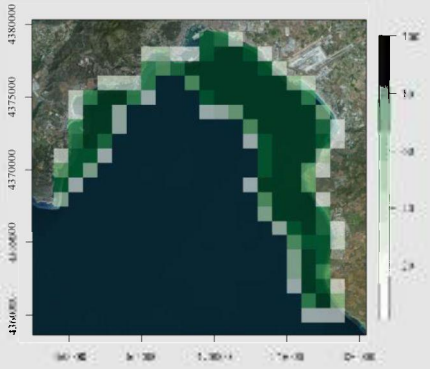


Figure 7.5 Spatial coverage of the monitoring area for each grid cell of 1 x 1 km resolution. Coverage is expressed in percentage.

Spatial coverage

Grid cells located in the edges of the study area had a portion of their surface that was not surveyed. Hence, we calculated the percentage of monitored surface for each grid. We used the original study area generated at 100 x 100 m in order to make the calculation, and assigned the spatial coverage to each 1 x 1 km grid cell (Figure 7.5).

Temporal coverage

We assessed the probability of detecting a boat in a given shipboard survey (*v*) using empirical data of the fishing patterns (i.e., effective fishing time) of boat anglers from an independent survey (Morales-Nin et al. 2005). First, we selected the interviews that correspond to boat fishing with hook and line (n = 290), and generated an empirical distribution of fishing time intervals (Figure 7.6 left). Second, we defined the monitoring time intervals for each survey using the starting and ending time of each one (n = 208, Figure 7.6 right). Then, we defined two independent time periods (morning and and afternoon) and calculated the time interval intersections between surveys and angler interviews. We considered as positive overlap those intersections with at least 30 min of overlap. Finaly, for each survey, the percentage of anglers that would be detected was calculated as the percentage of time overlap between the shipboard surveys and the interviews (Figure 7.6 right). For analysis, we filtered out those surveys with a percentage with <65 % of temporal coverage (n = 20), resulting in 188 surveys.

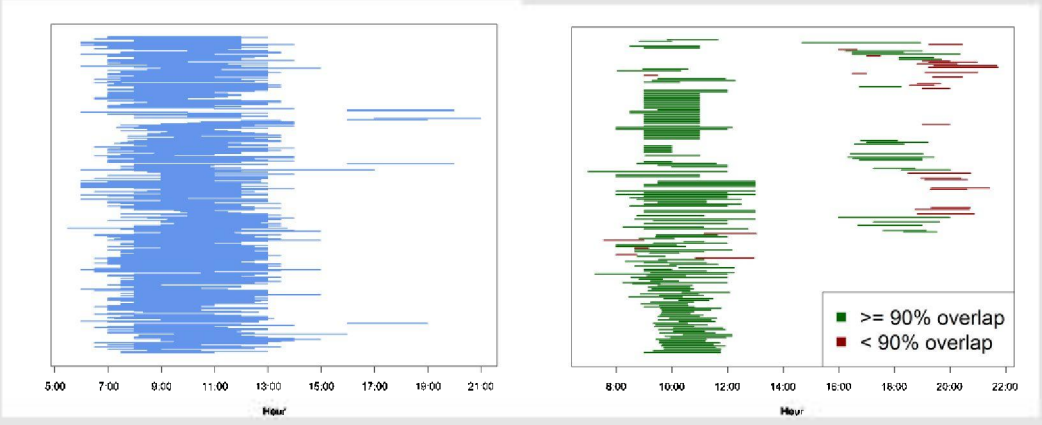


Figure 7.6 Left panel: Fishing time periods from boat anglers. Each horizontal line represent the time period of each boat angler (n = 290). Right panel: Shipboard survey time periods. Each horizontal line represent the monitoring time interval of each survey (n = 211). Colors represent the percentage of overlap of surveys with angler's fishing time periods.

Box 7.2 BRT optimization

BRT regularization to constrain over-fitting requires jointly optimizing three parameters: tree complexity (*tc*), learning rate (*lr*), and number of trees (*nt*). Learning rate determines the contribution of each tree to the growing model, thus affecting how quickly the model converges on a solution (i.e., decreasing *lr* increases *nt*). Tree complexity refers to the number of nodes in a tree, and controls whether interactions are fitted: a value of one fits an additive model, a value of two first a model with two-way interactions and so on (see Elith et al. 2008). An additional parameter, bag fraction (*bf*), determines the percentage of the data that is used for model building at each step. This incorporates stochasticity to the model, allowing the improvement of accuracy and reducing over-fitting (Friedman 2002). As rules of thumb, the combination of parameters should allow the BRT model to grow at least 1,000 trees (Elith et al. 2008), whereas high *tc* values (e.g. > 5) are not recommended (Dormann 2011).

To optimize the predictive performance of the hurdle model, we fitted the binomial and Poisson parts separately using all possible combinations of parameters as defined by: $lr \in [0.01, 0.005, 0.001, 0.0005]$, $tc \in [1, 3, 5]$, $nt \in [50, 100, \ldots, 15000]$, and $bf \in [0.5, 0.6, 0.7]$. The optimized model was that with the combination of parameters that minimized the a loss function (i.e.,, residual deviance) calculated with the independent testing dataset. Results for all combinations are provided for the binomial (Table D1 in Appendix D) and Poisson models (Table D2). Figure 7.7 illustrates the relationship between parameters, which was used for guiding the selection of optimal parameters. Note that, although the combination of $lr = 0.005$, $tc = 5$ and $bf = 0.7$ presented the minimum residual deviance for the Poisson part (Table D2 in Appendix D), the prediction error of this combination increased above ≈2000 trees, as more trees were added (i.e., the curve rise steeply after reaching a minimum, indicating overfitting). In contrast, smaller values for *lr* (i.e. lr = 0.001) approached similar predictive performance more slowly without exhibiting a steep rise after reaching the minimum error.

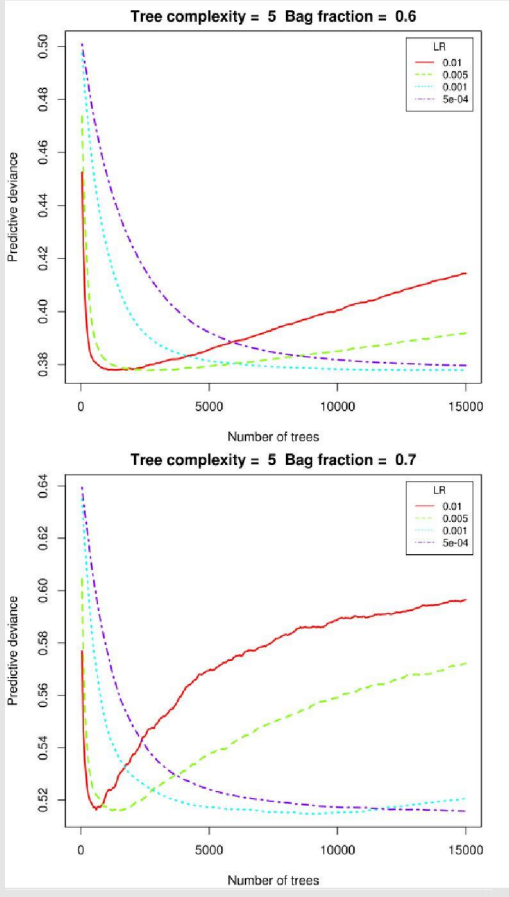


Figure 7.7 The relationship between tree complexity, learning rate and the predictive deviance for the binomial (top) and Poisson (bottom) parts of the hurdle model.

7.2.2 Numerical simulations

We estimated fishing harvest for each cell (i) and day (j) during a complete year (i.e., 2007) by combining predictions of fishing effort (i.e., the BRT) with the predictive model of YPUE developed in Chapter 6. Fishing effort estimates were provided in number of boats, whereas the YPUE model estimated yield

(g per angler per 30-min session). Consequently, it was required to transform the number of boat outings into number of anglers, while considering their fishing time, expertise and bait type used. Such transformation was achieved using empirical distributions of effective fishing time and number of anglers per boat. Because the YPUE model also accounted for two angling factors (i.e. angler expertise and bait type) different scenarios were considered. Bootstrap and randomization methods were used to account for uncertainty at the 95% confidence intervals. The following subsections provide additional details on each step of the process.

7.2.2.1 Predicting fishing effort

We used the hurdle model describe before (Section 7.2.1.4) to predict fishing effort (i.e., boat outings). We maintained the spatial offset term at the grid cell level (i), but the temporal coverage was set to 100% in order to provide an estimate of all boats fishing at a given time period. BRTs do not provide confidence intervals in their predictions; hence we used bootstrap methods (e.g., Leathwick et al. 2006). Bootstrap was implemented by resampling (n = 1,000) the training data set with replacement. This imply that all computational steps described from Equation 7.2 to Equation 7.7 were repeated 1,000 times. Parallel threads were used to optimize computational demands (see Box 7.3). Predictions were calculated for each grid cell (i), day (j) and period of the day (p). Boat outings predictions were provided in terms of mean estimates (μ_{ijp}). Therefore, the number of boats of each bootstrap was obtained by sampling once from a Poisson distribution with mean μ_{ijp}:

$$B_{ijp} \sim Poisson(\mu_{ijp}) \qquad \text{(Equation 7.2)}$$

Then, daily predictions resulted from the sum of the estimated values for the morning (p=1) and afternoon (p=2) periods:

$$B_{ij} = \sum_{p=1}^{2} B_{ijp} \qquad \text{(Equation 7.3)}$$

where B_{ij} is the number of boats per cell (i) and day (j)

Box 7.3 Computing facilities

Most of the analyses performed in this thesis were executed using a regular desktop computer (e.g. Inter Core 2 Duo CPU, 2.39GHz, 4GB RAM). However, bootstrap methods required high computational demands. The computing facilities of SOCIB (http://socib.es) were used to overcome such constrain. A computing server (Figure 7.8) with 2 Intel Xeon X5687 (3.60 GHz, quad-core) and 64GB RAM was used to run different scripts in R v.3.0.2. This configuration allowed to fit and predict multiple (up to 16 with hyper-threading technology) BRT models in parallel threads. We used the function *clusterApply* from the *parallel* package in R to accomplish such task. In addition, the 64GB RAM allowed to manipulate big arrays that were generated for storing the results of the simulations (i.e., 143 cells x 365 days x 1000 samples).

Figure 7.8 Computing server

7.2.2.2 Simulating angling factors

Variability on the fishing time and the number of anglers per boat were taken into account for estimating fishing harvest. First, for each predicted boat (b) at cell (i) and day (j) we simulated its fishing time:

$$S_b \sim S \quad \text{(Equation 7.4)}$$

where S_b, the number of 30-min time slots per boat (b), was simulated by random sampling from an empirical distribution of effective fishing time (S) obtained from onsite interviews (n = 390, see Figure 7.9a; Morales-Nin et al. (2005)). Second, for each boat (b) we also simulated the number of anglers:

$$A_b \sim A \quad \text{(Equation 7.5)}$$

where A_b, the number of anglers per boat (b), was simulated by random sampling from an empirical distribution (A) obtained from the shipboard surveys. The number of anglers per boat was found to be dependent on the business day and the season ($\chi^2(3, N = 2581) = 14.13$. $p < 0.01$), with higher number of anglers on non-business days and warm seasons (Figure 7.9 b and c). Therefore, eight different distributions accounting for each combination of business day (2-factors) and season (4-factors) were used.

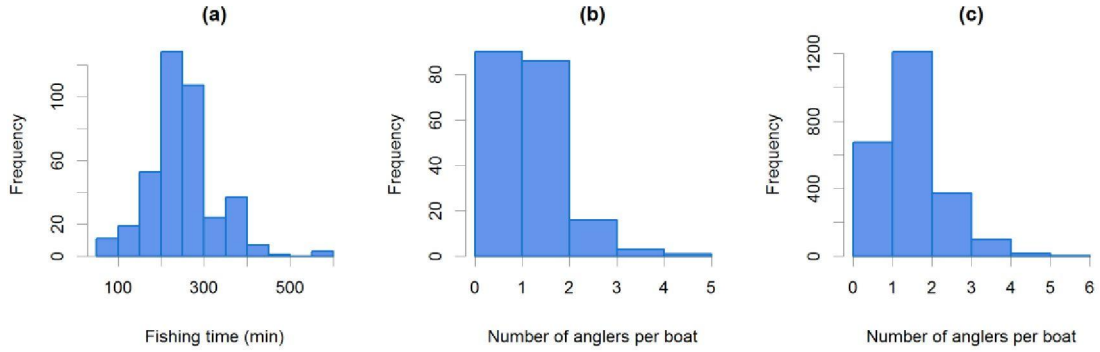


Figure 7.9 Empirical distributions of boat fishing patterns: a) effective fishing time (minutes); b) number of angler per boat (business day); c) number of anglers per boat (non-business day).

Angler expertise (i.e., expert or non-expert) and bait type used (i.e., worm or shrimp) were found to significantly affect YPUE (Chapter 6). We incorporated such individual variability by:

$$e_a \sim binom(p_e) \quad \text{(Equation 7.6)}$$

$$w_a \sim binom(p_w) \quad \text{(Equation 7.7)}$$

where e_a and w_a were the expertise and bait types assigned to angler (a), respectively. Both factors were obtained by sampling two binomial distributions with probabilities of being 'expert' (p_e; the probability of beign 'non-expert' is 1-p_e) and use 'worm' (p_w; the probability of use 'shrimp' is 1-p_w). Because of the lack

of empirical data on those probabilities, we considered five different scenarios. Four of them consisted of the four possible combinations assuming that the probability for each factor is 100% (e.g. 100% probability of being 'expert' and use 'worm'). The fifth scenario assigned two different proportions supported by two previous independent surveys. First, the proportions of worm (26%) and shrimp (74%) were obtained from a previous onsite survey (n = 414, Morales-Nin et al., unpublished data), where anglers were asked about the bait type used. Second, the proportions of expert (9%) and non-expert (91%) anglers were calculated from a previous survey (n = 165, Cardona et al., unpublished data). Expert anglers were defined as those anglers with more than 10 years of expertise and with a membership in a sport club.

7.2.2.3 Predicting fishing harvest

Finally, we estimated the fishing catch for each angler (a) using the predictive model of fishing quality developed in Chapter 6. Such model provided estimates of YPUE (i.e. g per angler per 30-min session) and took into account spatial (i.e. depth) and temporal (i.e. SST) information together with the two above mentioned angler factors (expertise and bait types). Bootstrapped predictions (n = 1,000) for each combination of angler factors were generated (i.e., 4000 estimates per grid cell (i) and day (j)). Bootstrap samples were produced taking into account, not only the uncertainty in the model parameters, but also the stochastic variation considered by the random factors (i.e., cell and day) and the residual variation. This allowed incorporating model uncertainty into yield estimates:

$$YPUE_{ijbsa} \sim YPUE^{*}_{ijwe} \quad \text{(Equation 7.8)}$$

where $YPUE_{ijbsa}$ is the yield of angler (a) per time slot (s) at boat (b), and it was sampled from bootstrapped estimates of YPUE ($YPUE^{*}_{ijwe}$) at cell (i) day (j) for the same expertise (e) and bait (w) types assigned to angler (a). Then, total harvest for angler (a) can be calculated as:

$$H_{ijba} = \sum_{s=1}^{S_b} YPUE_{ijbsa} \quad \text{(Equation 7.9)}$$

where S_b is the number of 30-min time slots of boat (b). Therefore, total harvest per cell (i) and day (j) can be obtained by:

$$H_{ij} = \sum_{b=1}^{B_{ij}} \sum_{a=1}^{A_b} H_{ijba} \quad \text{(Equation 7.10)}$$

where A_b is the number of anglers per boat (b), and B_{ij} is the number of boats per cell (i) and day (j). Finally, both fishing effort and fishing harvest were calculated with their 95% confidence intervals at three levels of aggregation: 1) on a daily basis (i.e., by summing all grid cells [143] for each day (j)); 2) at the grid cell level (i.e., by summing all days for a given cell (i)); and 3) at the entire study area per year:

$$B = \sum_{i=1}^{143} \sum_{j=1}^{365} B_{ij} \quad \text{(Equation 7.11)}$$

$$H = \sum_{i=1}^{143} \sum_{j=1}^{365} H_{ij} \qquad \text{(Equation 7.12)}$$

7.3 Results

7.3.1 Spatio-temporal patterns of boat anglers

Relative contribution (RC) of each explanatory variable for either the binomial and Poisson models is presented in Table 7.1. The response of each of the top six explanatory variables is illustrated with the partial dependence plots for both the binomial (Figure 7.10) and the Poisson (Figure 7.11) models. Angler boat occurrence, as modelled with the binomial part, was mainly influenced by a combination of temporal and spatial variables. Main temporal variables included calendar (i.e., business day) and weather conditions (i.e., wave height). Occurrence probability was higher during morning periods, non-business days and calm sea conditions. Wave height exhibited a non-linear response with a threshold effect close to 0.5 m (Figure 7.10). Probabilities of finding a boat above such threshold were minimal. On the other hand, spatial variables were mainly related to accessibility. Boat occurrence presented a non-linear response to the shore distance and diminished with decreasing accessibility from ports (i.e. as result of the gravity model). For the Poisson part, other spatial variables such as depth and the coverage of seagrass presented high RC.

BRT optimization showed that higher tree complexities (i.e,. $tc = 5$) performed better than models that did not account for interactions between variables (i.e., $tc = 1$). The relative strength of the interactions between explanatory variables is presented for both the binomial (Table D3 in Appendix D) and the Poisson parts (Table D4 in Appendix D). Relative strength values for the Poisson parts were low (i.e., a value of zero indicate that no interactions effects were fitted). In contrast, relative strength values from the binomial part were higher. The top five interactions (Table D3 in Appendix D) included the most influential predictors as seen by their RC. In particular, port-based accessibility was found on the top four interactions. Partial dependence plots for four of the most relevant interactions are shown in Figure 7.12.

7.3.2 BRT model performance

The BRT models showed good overall agreement between observed and predicted data (Table 7.2). There were differences between the training and testing data sets, with more accurate estimates for the former, as expected. Results of model performance for the training and testing data sets are presented in Table 7.2. The explanatory power of the binomial part was robust (AUC = 0.85) and model residuals did not present spatial autocorrelation (Moran's I = 0.004 ± 0.026). The optimized hurdle model explained 32% of the deviance in the density of boat counts, and there was no evidence of spatial autocorrelation in the residuals as well (Moran's I close to zero, Table 7.2). Aggregation of the number of boat counts at temporal (i.e., number of boats per survey by pooling all grid cells) and spatial levels (i.e., number of boats per grid cell by pooling all surveys) outperformed model predictions at the cell level (Table 7.2). Figure 7.13 shows the maps of observed and predicted number of boats by pooling all surveys, for both training and testing data sets.

Table 7.1 Predictor variables included in the hurdle model and their relative contributions (RC, in percentage) to the binomial and Poisson parts. Numbers in bold highlight the top six variables to a given model.

Abbreviation	Description (units)	$RC_{binomial}$ (%)	$RC_{poisson}$ (%)	Source
Temporal				
Tmax	Daily maximum temperature (ºC)	**6.5**	2.6	1
Prec	Daily precipitation (mm)	1.3	0	1
Sun	Solar hours (h)	2.8	**9.7**	1
Wmed	Average wind speed (kmh^{-1})	2.5	4	1
Hm0	Significant wave height (m)	**8.9**	4.7	2, 3, 4
busD	Business day	**10.4**	0	5
Morning	Morning-Afternoon	3.3	0	
Month	Month	1.1	1.1	
Year	Year	5.9	3.3	
Spatial				
Depth	Mean depth (m)	2.1	**9.6**	6
hSgrs	Seagrass coverage (%)	4.7	**11.7**	6
hRock	Rocky bottoms (%)	2.7	2.8	6
dCoast	Closest distance to the shore (m)	**8.2**	4.1	6
dNat	Closest distance to natural areas (m)	3.1	4.8	7, 8
dPort	Port-based accessibility	**15.8**	**16.4**	8
Spatio-temporal				
Cpue	Catch per unit effort (individuals)	4.4	6	6
Ypue	Yield per unit effort (g)	3.9	**7.4**	6
MLt	Average fish size (mm)	**7.2**	4.8	6
Shan	Fish diversity (Shanon index)	4.3	**6.5**	6
MPA	Marine protected area	0.9	0.5	5, 9

Sources: 1, National Meteorological Agency (AEMET, http://www.aemet.es); 2, Jorda et al. 2012; 3, Martínez-Asensio et al. 2013; 4, Puertos del Estado (http://www.puertos.es); 5, Official Bulletin of the Balearic Islands (BOIB, http://www.caib.es/boib/); 6, Chapter 6; 7, Balaguer et al. 2008; 8, This Chapter; 9, Natural Resources Service of the Government of the Balearic Islands.

Table 7.2 Predictive performance of the binomial and hurdle models on the training and testing data sets. Hurdle model is analysed at three aggregation levels. Note that Moran's I is calculated only for models with spatial component, and no standard deviation (s.d.) is provided at the "Spatial" aggregation level. Area under curve (AUC) is calculated for the binary responses, whereas Pearson's correlation coefficient (r) and root-mean-squared error (RMSE) for count estimates.

Model	Data set	Deviance explained (%)	Moran's I (mean ± s.d.)	AUC	r	RMSE
Binomial						
Spatio-temporal ($_{i,j}$)	Training	37.7	0.003± 0.024	0.926	-	-
	Testing	22.9	0.004 ± 0.026	0.852	-	-
Hurdle						
Spatio-temporal ($_{i,j}$)	Training	49.1	0.004 ± 0.023		0.536	0.439
	Testing	32	0.005 ± 0.026		0.379	0.443
Spatial ($_{i}$)	Training	85.893	-0.021		0.955	4.643
	Testing	62.2	-0.004		0.808	4.459
Temporal ($_{j}$)	Training	85.9	-		0.933	5.478
	Testing	58.4	-		0.748	9.003

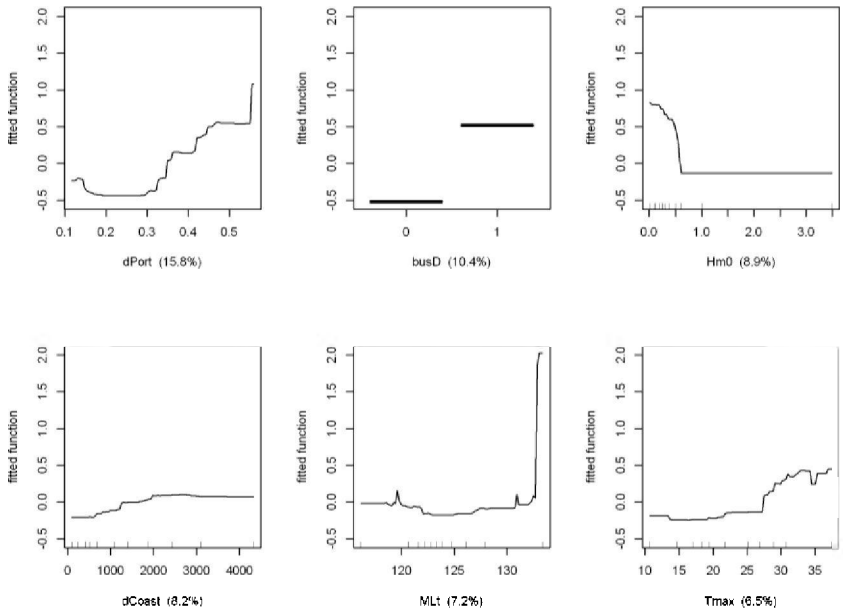


Figure 7.10 Partial dependence plots of the top six variables from the binomial part of the hurdle model. Relative contribution in percentage is provided between parentheses for each variable. See Table 7.1 for variable's abbreviations.

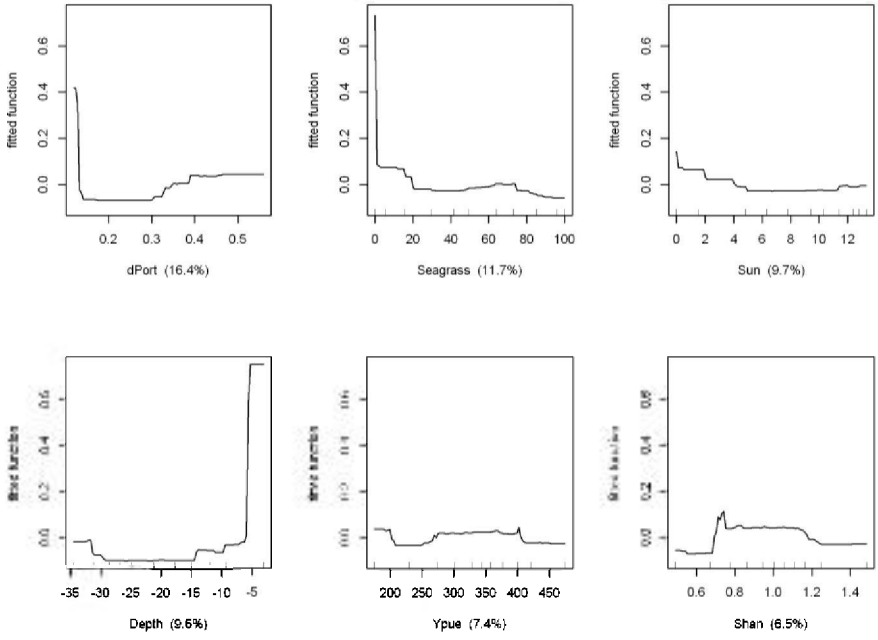


Figure 7.11 Partial dependence plots of the top six variables from the Poisson part of the hurdle model. Relative contribution in percentage is provided between parentheses for each variable. See Table 7.1 for variable's abbreviations.

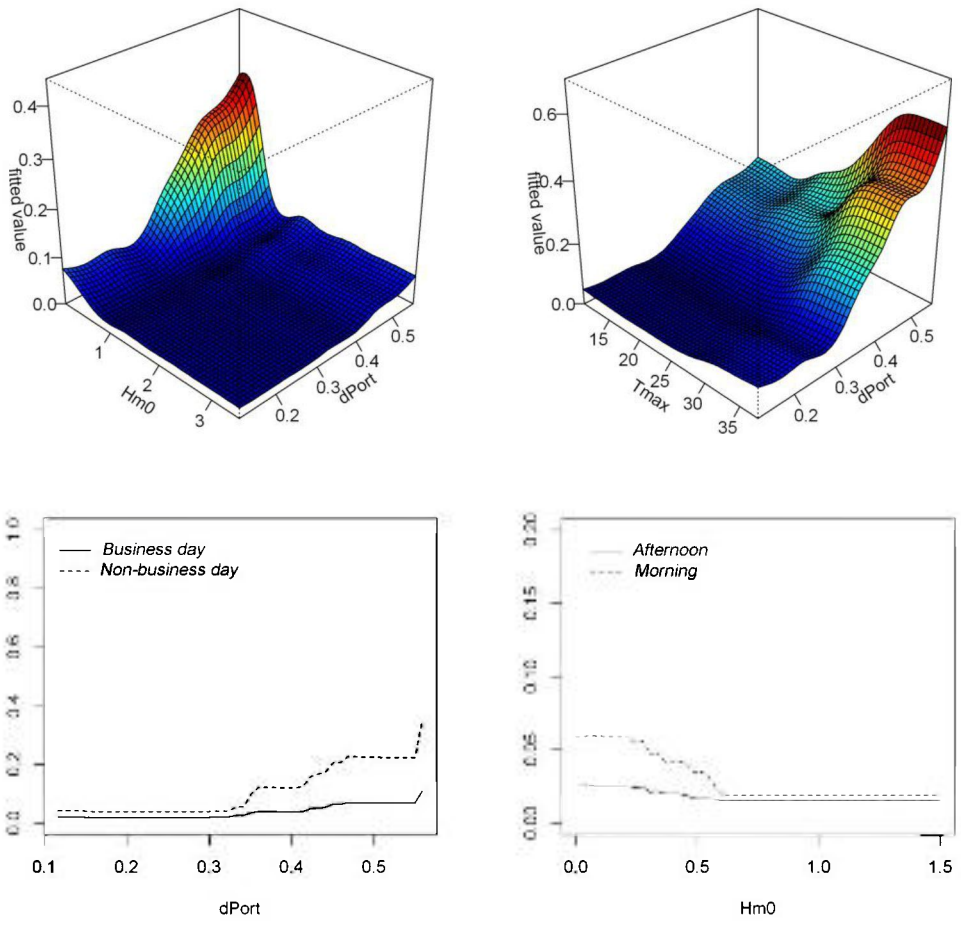


Figure 7.12 Partial dependence plots for main strongest interactions in the binomial model. Vertical axis represents the predicted values for the two predictors, with values for all other variables set at their mean. Note that vertical axis is rescaled on each plot to improve visualization. Top plots represent three-dimensional surfaces of the interactions between port accessibility (dPort) with wave height (Hm0) and maximum air temperature (Tmax). Bottom plots illustrate the interactions between port accessibility and business day (bottom-left) and between wave height and period of the day (morning or afternoon).

7.3.3 Fishing effort and fishing harvest

The fishing effort for 2007 at Palma Bay was estimated in a total of 5,008 boat outings (range 95% CI: 4,031-6,221). The spatial distribution of fishing effort (i.e., median and 95% CI range) is presented in Figure 7.14a-b, whereas the daily temporal pattern across the entire year is also presented in Figure 7.14c-d-e.

Total harvest estimates (i.e., considering the five scenarios) for 2007 at Palma Bay are presented in Figure 7.16. As expected by the YPUE model, higher values are estimated for the scenarios with expert anglers and worm. Moreover, there is no overlap in harvest estimates between scenarios with different

angler expertise. However, those four scenarios represented the more extreme combinations. In contrast, the fifth scenario combined more plausible proportions of both angler and bait types. Total harvest for such scenario was 23.9 t per year (range 95% CI: 19.3-29.4). For illustrative purposes the spatial and temporal distributions of that scenario are presented in Figure 7.15. Note that, since angler factors did not interact with environmental variables in the YPUE model, no differences in the spatial and temporal distribution are present among scenarios.

7.4 Discussion

In this Chapter we have proposed a novel approach for estimating fishing harvest in a spatially-structured marine recreational fishery. Recent advances on habitat and fishing quality mapping (i.e., Chapter 3 and Chapter 6), together with advanced modeling techniques (Magnusson et al. 2013, Soykan et al. 2014) have provided an unprecedented opportunity to assess the spatio-temporal patterns of fishing effort and fishing harvest. The present work has demonstrated the use statistical models to predict the spatio-temporal patterns of recreational fishers within complex socio-ecological systems. Using empirical data, angler site allocation and participation were modelled as a function of physical, biological and social components. The utilization of BRT has been proven useful for taking into account complex effects such as non-linearities, threshold effects and interactions between factors in order to provide robust estimates of fishing effort. In combination with a catch-related model based on fishery-independent measures and bootstrapping methods, the proposed geospatial framework has allowed to provide estimates of the total harvest together with a quantification of uncertainty measures. Overall, our framework proposes a new tool, mainly based on fishery-independent data, which provide a deeper understanding on how anglers exploit spatially-structured resources. Such approach can be applied to any other human-prey system worldwide, including fishing or harvesting, and contributes to defining the basis of sustainable exploitation.

7.4.1 Fishing effort allocation

The first module of the framework proposed in this work relies on the prediction of angler behaviour, specifically, site choice allocation. Previous studies identified different attributes that can affect angler site choice and participation, maximizing personal utility (e.g., Hunt 2005, Johnston et al. 2010). Our results indicate that angler occurrence was mainly related to accessibility, weather conditions, and social factors like non-business days. The threshold identified for wave height conditions (i.e., 0.5 m wave height) was similar to a previous boat angling study (Cabanellas-Reboredo et al. 2014). In that study, wave conditions also resulted in one of the main predictors for fishing effort, thus highlighting the relevance of weather conditions in predicting recreational activities.

Port-based accessibility was one of the major predictors in our model. This fact is in agreement with previous studies. For example, the lobster angler fishery in Tasmania was found to be distributed near to access points (Stuart-Smith et al. 2008). Also in Palma Bay, the recreational squid fishery distributed according to port distance as well (Cabanellas-Reboredo et al. 2014). In fact, distance to access points has been considered as one of the major predictor of angler's site choice (Hunt 2005). Accessibility can be representative of travel cost (Matsumura et al. 2010), but also can be understood as an attribute of safety

(Norse 2010). Unlike previous studies where distance to the closest port is usually calculated (Stuart-Smith et al. 2008, Cabanellas-Reboredo et al. 2014), here we used a gravity model, which proven to be a useful predictor of fishing effort allocation when prior information of the port origin is unknown. Port-based accessibility was also a key variable when modeling interactions between variables. Results indicated that, when favourable temporal conditions (i.e., low wave height, higher maximum temperature, non-business day or morning period), there was a higher proportion of anglers fishing in more accessible locations. However, the difference between accessible and remote areas was lower in non-optimal conditions. This effect could be explained by considering that anglers that went fishing in non-optimal conditions were mainly driven by catch-related factors rather than other comfort factors like accessibility. This hypothesis would be in agreement with a previous work on the recreational squid fishery, where catch-related variables were more determinant than calendar variables in the allocation of fishing effort (Cabanellas-Reboredo et al. 2014). In fact, fishing quality metrics appeared to play a secondary role in the present study. Although partial dependence plots suggested that anglers would prefer locations with higher fish lengths, angler response to other fishing quality metrics was rather unclear. The higher angler participation in summer months is certainly more plausible due to better weather conditions and social factors like bank holidays rather than higher fish biomass. In general, results suggest that the studied fishery is mainly driven by leisure motivations in contrast to other recreational or commercial fisheries, mainly driven by catch-related factors.

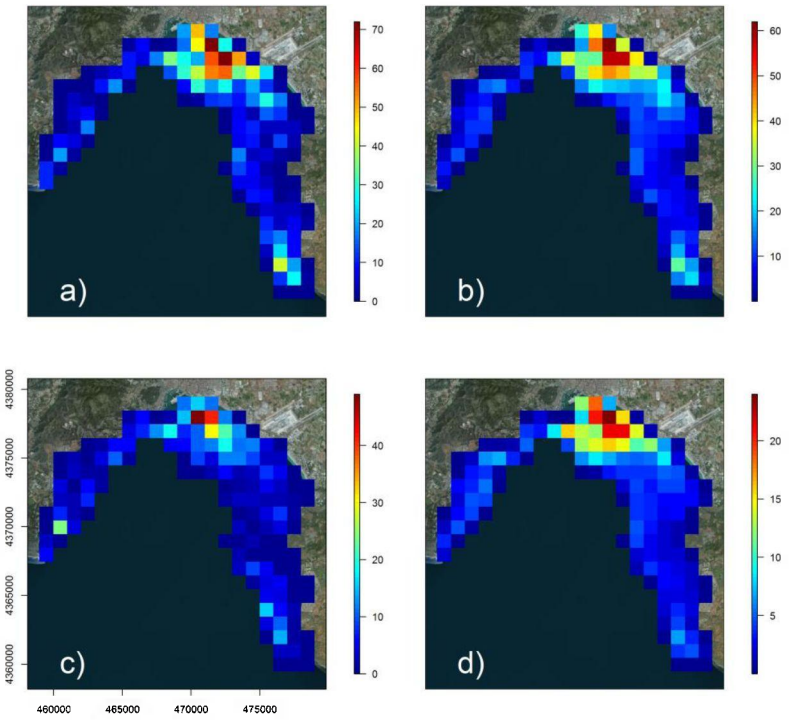


Figure 7.13 Observed and predicted estimates of aggregated boat counts per grid cell for all surveys: a) observed values in the training set; b) predicted estimates for the training set; c) observed values in the testing set; d) predicted estimates for the testing set.

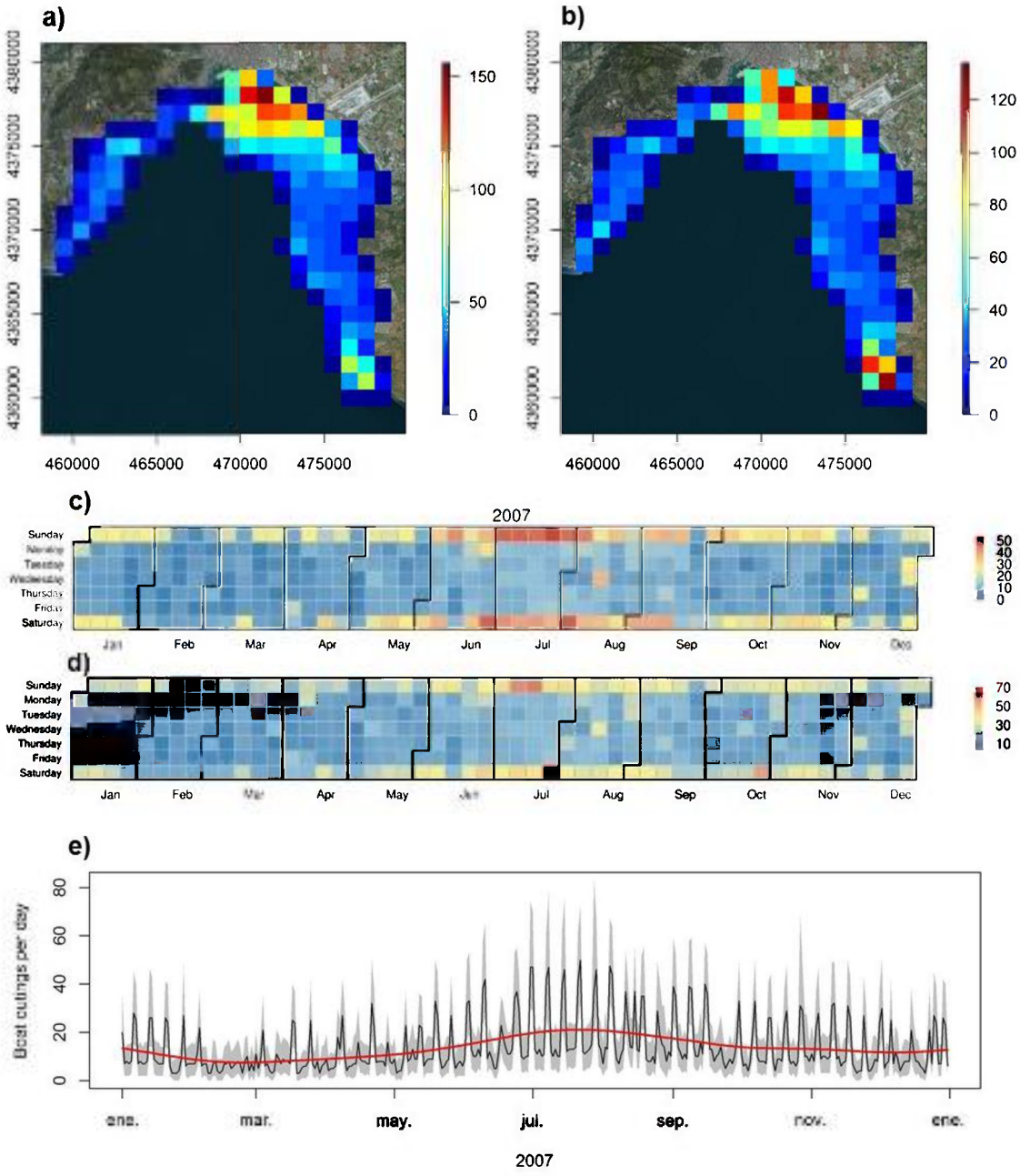


Figure 7.14 Predictions of fishing effort (boat outings): a) total number of boat outings per grid cell per year (median estimate); b) total number of boat outings per grid cell per year (95% CI range); c) boat outings per day for the entire study area (median estimate); d) boat outings per day for the entire study area (95% CI range); e) boat outings per day for the entire study area (black line represents the median, grey boundaries correspond to the 95% CI range, and red line is a cubic smoothing spline indicating the seasonal trend).

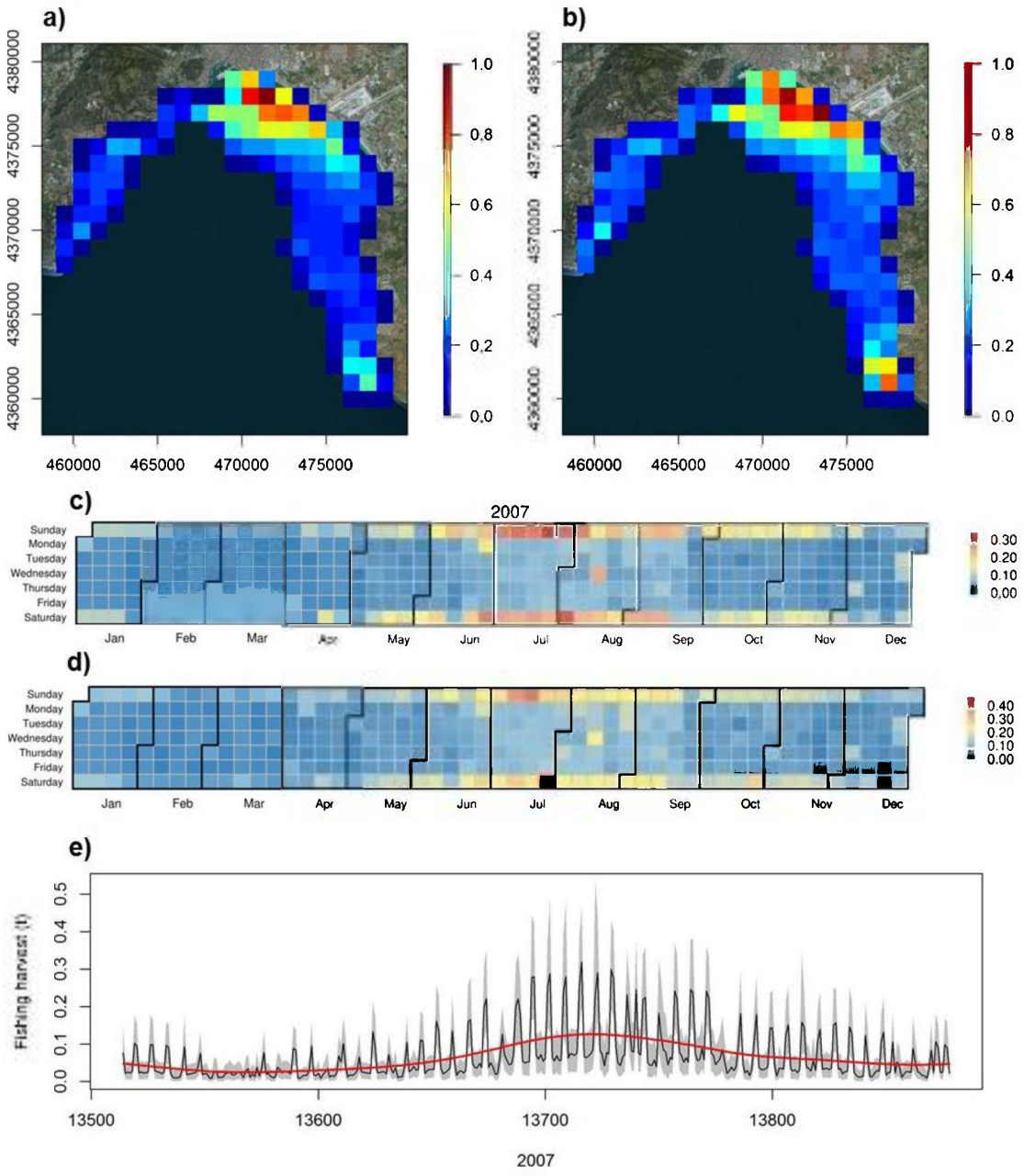


Figure 7.15 Predictions of fishing harvest (in tons) for the scenario with mixed composition of angler and bait types: a) total harvest per grid cell per year (median estimate); b) total harvest per grid cell per year (95% CI range); c) harvest per day for the entire study area (median estimate); d) harvest per day for the entire study area (95% CI range); e) harvest per day for the entire study area (black line represents the median, grey boundaries correspond to the 95% CI range, and red line is a cubic smoothing spline indicating the seasonal trend).

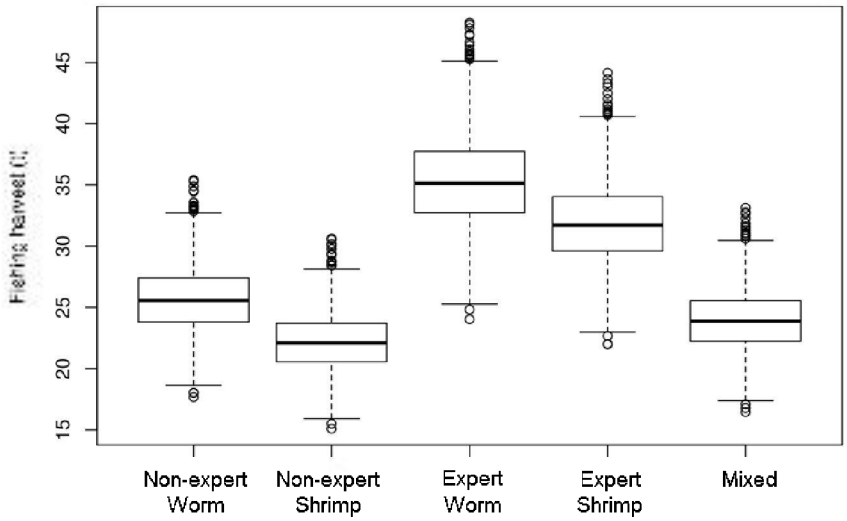


Figure 7.16 Fishing harvest at Palma Bay estimated in five scenarios for the year 2007. Boxplot of the 1,000 bootstrapped values for each of the five scenarios. The first four scenarios consider the combination of one type of angler (i.e., expert and non-expert) with one bait type (i.e., worm and shrimp). In contrast, the fifth scenario considers combined proportions with 91% of non-experts and 74% of anglers using shrimp.

Model prediction presented an overall good performance. Performance was lower when predicting at the grid cell and day level. Such error is reasonable due to the high stochasticity of complex systems like human behaviour, and is affected by the temporal and spatial scales. However, results outperformed when assessing model performance at different aggregated levels (i.e., all boats per day or all boats per grid cell).

Observed data and model predictions provided evidences that fishing effort exhibited a heterogeneous spatial distribution across Palma Bay. The main areas of concentration were located in the northern part of the bay, where there was a higher concentration of ports and marinas. Other areas that concentrate a higher fishing effort were located in more remote locations, close to natural areas. The predicted number of fishing trips (i.e.,, 5,008 outing year^{-1}) would represent a 1.3% of the estimates (387,001 outings year^{-1}) reported for the whole island and considering all boat-based recreational fisheries (Morales-Nin et al. 2005). However, this comparison need to be taken with care since the methodological approaches were different. On the other hand, a previous study (Cabanellas-Reboredo 2014) provided higher estimates for the squid fishery, another boat-base modality, at Palma Bay with 15,767 outings year^{-1} (95% CI: 15,015-16,626) using a similar approach; thus highlighting the need for assessing fishing effort by fishing modality.

7.4.2 Fishing harvest

The second part of the framework proposed here is the numerical method for estimating the spatio-temporal pattern of fishing harvest. The method relied on the combination of two models, one for predicting fishing effort (i.e. boat outings) and the other for predicting YPUE (g per angler per 30-min).

Therefore, the key point was to transform boat outings into anglers with their respective fishing times. The incorporation of empirical distributions allowed such transformation. In addition, the use of bootstrap and randomization methods allowed the propagation of uncertainties across each step. Since the model of YPUE also considered angler factors such as expertise and bait used, incorporating such information in terms of different scenarios was the selected option in front of the lack of empirical data. The differences obtained between scenarios allowed representing different extremes, while pointing out the need for further studies focusing on the characterization of angler's characteristics. Despite the differences between scenarios, the spatial heterogeneity of fishing harvest was mainly influenced by the distribution of fishing effort. Temporal distribution was very similar as well, but with slight differences in winter time when fish biomass was lower.

A previous study used commercial landings and reported that the artisanal fishery took a capture of 587.31 t in 2008 in Mallorca island (Morales-Nin et al. 2010). We filtered out the same database (Palma wharf; OpMallorcamar) by those species (i.e., in terms commercial categories) that matched with main target species (i.e. 10 most abundant species from list in Table 6.2), and estimated that the artisanal fishery would have captured 86.7 t in 2007 in Mallorca island. Therefore, taking into account the mixed scenario as the most plausible (23.9 t), the recreational fishery at Palma Bay would represent 27.6% of the total artisanal catch over the seagrass fish community in Mallorca. This point highlights the need to consider recreational fisheries in fisheries management and not consider negligible its impact.

7.4.3 Limitations and future directions

Harvest estimates should be taken with caution since they rely on several assumptions. First, we did not consider catch-and-release practises, mainly due to the lack of data. However, this fishery is consumptive oriented and the proportion of fish released, although unknown, is expected to be low. In addition, although high proportions of undersized fish have been reported (Alós et al. 2008), post-release mortality estimates (Alós et al. 2009) supports that some mortality of fish released should need to be taken into account. Second, catch estimates were based on the model presented in Chapter 6, where combinations of angler factors such as gear, bait type and angler expertise were limited by the experimental design. Those combinations may not represent the complexity of angler types and gears. Nevertheless, our modeling approach is flexible enough to accommodate new data whenever available.

Future works should be directed towards the incorporation of individual-based information and coupling statistical models like SDM with mechanistic or process-based models. Such approach could incorporate information regarding fishing tactics (eg. anglers that switch between modalities), historical catch success and spatial memory, gear characteristics, angler performance, boat characteristics, movement and information transfer as well (eg. social networks). Such kind of information is currently available for some commercial fisheries through electronic logbooks and vessel tracking systems. The recent development of citizen science applications using mobile devices could be one possible solution for the case of recreational fisheries. In addition, the recent development of high resolution models of hydrographic conditions, together with the advent of new observing systems (e.g., Tintore et al. 2013), could provide new insights into the angler response to environmental factors.

Consideration of the spatio-temporal variability of human activities at sea is key for the implementation of Marine Spatial Planning and holistic assessments of the cumulative pressures. The geospatial approach used here could be applied not only to other marine recreational fisheries but also to small scale commercial fisheries, which are also characterized by incomplete monitoring data. Spatial monitoring of fishing effort allows the identification of hot spots in order to evaluate recreational fishing impact. Our modeling approach may be used to assess fisher's response to management measures and investigate the effects of different management scenarios including multiple regulations (e.g., catch-and-release enforcement, gear restrictions, temporal closures, MPA). In addition, information on spatio-temporal patterns of recreational anglers could be used to optimize fishery control efforts. This aspect can be relevant in the Mediterranean, where enforcement of management rules is weak, especially due to the limited control of maritime activities (Morales-Nin et al. 2010).

Acknowledgements

This work would not have been possible without the help and support of the volunteers that collaborated in the shipboard surveys. We thank Beatriz Morales-Nin and Federico Cardona for providing interviews databases, Gabriel Jordà and Puertos del Estado for providing the wave models, and Pau Balaguer for providing the shoreline characterization data. This study was financed by the projects ROQUER (CTM2005-00283) and CONFLICT (CGL2008-958), which were funded by the Spanish Ministry of Research and Science. Additional support has been received from RECUMARE and PERSEUS projects.

SECTION V. DISCUSSION AND CONCLUSIONS

Chapter 8
General discussion

8.1 General discussion

This thesis demonstrated how to integrate of biotic, abiotic and human components in order to support the implementation of the principles of the ecosystem approach to fisheries management (EAF). The combination of information on benthic habitat, fish movement, fishing quality and angler behaviour provided the basis for estimating recreational fishing effort and harvest using an original approach. On the one hand, the distribution of benthic habitats, together with other biophysical information, contributed to the identification of the essential fish habitat (EFH) of the main target species. In turn, this information was used for designing the experiments of fish mobility and for modeling the spatial distribution of fishing quality as well. The quantification of fish home ranges offered empirical information for defining the proper spatial scale of observation units for the analysis of angler site choice and the quantification of fishing effort and harvest. On the other hand, fishing quality metrics were used for modeling angler site choice and assessing whether catch-related variables played a key role in the distribution of recreational anglers. Finally, all previous information was combined to estimate the spatio-temporal patterns of recreational fishing effort and harvest.

Results showed that the spatial distribution of recreational anglers is heterogeneous, with some areas that concentrate higher fishing effort. This information could be used with different objectives. On the one hand, information on site choice can be used for stratifying further monitoring programs and optimizing fisheries controls. Previous studies have described conflicts or interactions with other maritime activities like artisanal fisheries (Cardona 2011) or recreational activities like boating or diving (Lynch et al. 2004, Morales-Nin et al. 2010). Therefore, information related to the spatial distribution of recreational fisheries can be incorporated into marine spatial planning process or cumulative pressure assessments (Halpern et al. 2008, Levin et al. 2009).

One of the main challenges found when facing socio-ecological models in general, but decisively in the case of recreational fisheries, is the lack of data of environment and human activities at adequate spatial and temporal scales. This issue is highlighted by different European data policies (i.e., INSPIRE Directive, Marine Knowledge 2020). The development of spatial data infrastructures (e.g., EMODnet, Cinnirella et al. 2012) and new integrated observing and forecasting systems (EC 2013b, Tintore et al. 2013) are already becoming instrumental in providing reliable data. In our case, the incorporation of biotic, abiotic and human components into the different spatial models implied to combine variety of data sources. In addition to the information generated with the fieldwork activities; data from third-parties was obtained as well (e.g. meteorological and oceanographic information). In fact, one of the successes of this work was the integration of different data types. Multiple instruments used (see Box 8.1) measured different parameters (e.g. fish detections, boat anglers, water temperature, etc.), which in turn were represented using different data typologies (e.g. points, lines, polygons, rasters), and generated in different formats (e.g. csv,

netCDF, shapefile). Dealing with all this data heterogeneity constituted one of the main challenges of this thesis.

It's worth mentioning the impact that some of the works presented in this thesis had in subsequent studies. One the one hand, the developed drop-camera system (Chapter 2) was used in another study for determining benthic habitats as well (Alós and Arlinghaus 2013). The benthic habitat map generated in Chapter 3 was used as predictor variable for analysing the spatial patterns of the squid fishery (Cabanellas-Reboredo et al. 2014) and for assessing local-scale fish larval connectivity (Basterretxea et al. 2012). One the other hand, the pioneering implementation of the acoustic tracking network at Palma May Marine Reserve resulted in subsequent studies (Alós et al. 2011, Alós et al. 2012a, Alós et al. 2012b, Cabanellas-Reboredo et al. 2012, Gil-Oviedo 2013). Future research on this field should be oriented towards the long-term assessment of fish movement patterns. In this regard, development of smaller transmitters with higher battery capacity is a key factor for providing further opportunities.

Box 8.1 Ocean observing and modeling systems

This is an overview of different platforms and models that were used along this thesis:

Numerical models: Mathematical simulations of ocean dynamics and processes. They were used to provide wave estimates on a daily basis (WANA & IMEDEA, Chapter 7), general patterns of water residence time (WRT, Chapter 3) and near-bottom orbital velocities (U_b, Chapter 2 and Chapter 3).

Fixed stations: Fixed platforms taking point observations of different weather and oceanographic variables. They included weather stations (Chapter 7), oceanographic buoys (Chapter 4 & Chapter 7), and acoustic listening stations (Chapter 4 and Chapter 5).

Remote sensing: Earth observations from aerial sensors, like aircrafts or satellites, or underwater sensors towed from a boat. They include simultaneous multi-spectral platforms from satellite such as Landsat (Chapter 3), aerial imagery (Chapter 3), side scan sonar (Chapter 2 and Chapter 3), and the developed drop-camera system (Chapter 2).

This thesis opens the door to future research. There are still some gaps that need to be resolved in relation to the ecosystem approach to fisheries (EAF). One the one hand, additional components of the socio-ecological system could be incorporated. For example, stock information derived from conventional approach developed for commercial fisheries would allow evaluating the proportion of the total harvest estimated in this work in relation to total biomass or abundance. In this regard, long-term monitoring programs would be needed. In addition, based on the information generated from this work, the characterization of areas of high and low fishing effort can be taken into account in further studies considering direct or indirect impacts of recreational fishing on marine ecosystems (Font and Lloret 2014). Results indicate that seagrass meadows and rocky habitats sustain target fish species of the recreational fishery, hence offering a valuable ecosystem service to society. In addition, the reduced mobility of fish species implies that the exploited resource is exposed to local impacts, and supports the idea of using sedentary littoral fish species as indicators of the health status of the ecosystem. Therefore, conservation of seagrass meadows is a major objective for the sustainable development of the recreational fishery.

Results from Chapter 6 and Chapter 7 highlight the need of taking into account angler characteristics (e.g. expertise or bait type). Therefore, future studies should assess angler segmentation in this regard. Acquisition of combined information on angler orientation profile together with spatial-explicit fishing activity patterns (i.e. including site allocation and fishing tactics) supposes a major challenge. Individual-based information could be obtained by logbooks. The recent advent of citizen applications using mobile devices and gamification methods opens new opportunities. Such vision may be unrealistic now for the recreational fishery studied here, since the main participants are middle-aged males (46 ± 2 years; Morales-Nin et al. 2005) and the use of smartphones, especially at sea, is limited. However, we can envisage a near future where new angler generations will use mobile applications for sharing their catch data with friends and tracking their activities, as other sport practisers do. Engagement with recreational anglers and other stakeholders as well (e.g. public administration, ports) will become a key factor for its success.

Another major challenge, not possible to overcome in this thesis, was the automatic classification of seabed images. Despite the prototype succeed in providing standardized vertical images (i.e. same angle, same height from the bottom); the lighting system was not able to offer a homogeneous illumination for the entire frame. This resulted in images that were not suitable for automated image classification. Future camera prototypes should have to take this issue into account. In addition, image classification of complex structures is a major challenge by itself within the domain of computer science. Preliminary analysis with the same images conducted by the System, Robotics and Vision Group from UIB provided promising results (Massot and Oliver 2013). Recognition of habitat types and estimation of seagrass cover would offer the camera system an outstanding added value. In addition, the development of new autonomous underwater vehicles (Figure 8.1) offer promising opportunities for benthic habitat mapping.

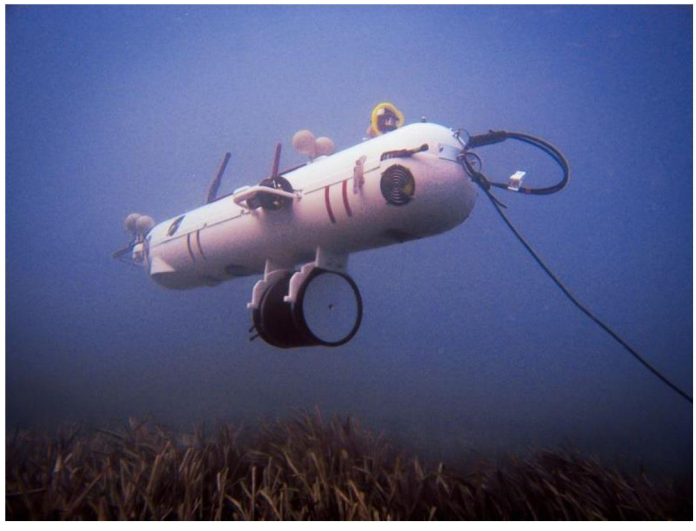


Figure 8.1 Autonomous Underwater Vehicle "Nessie-VI" carrying a camera system during the sea trials held at Palma Bay in October 2011

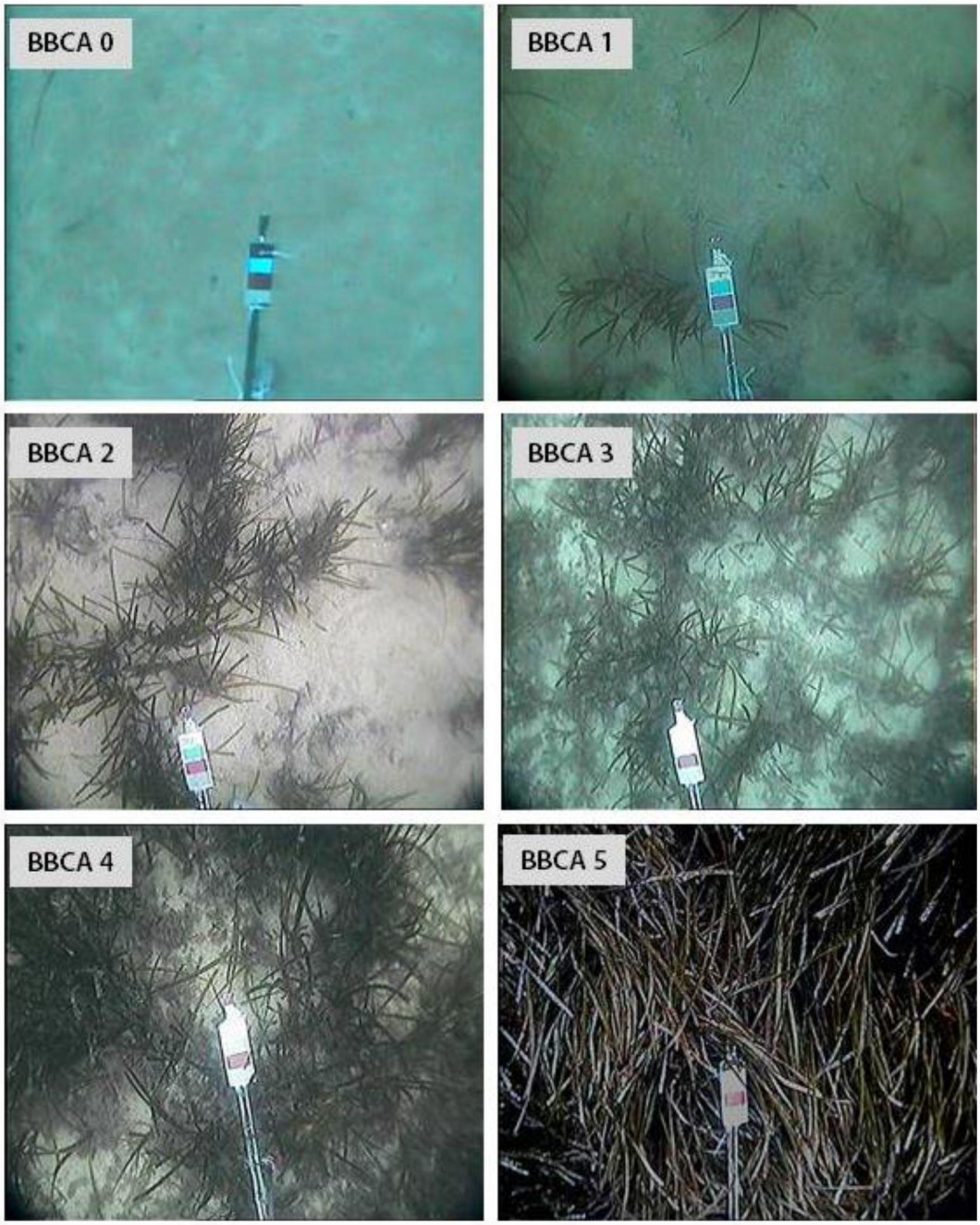
Information provided in this thesis could be used to guide adaptive policies and support fisheries management in different applications. As mentioned in different Chapters, the development of new tools and methods could support the development of science-based tools for decision making. Our ability to model fishing behaviour has a great potential for assessing different management scenarios and actions. However, putting all these tools together and in practise is a major hurdle. It is necessary to define clear management objectives and engage different stakeholders which, in turn, can also contribute to improve scientific models (Rassweiler et al. 2014). In addition, recent advances in computer science and cloud systems, which allow processing big amounts of data in outstanding computing times, offer encouraging opportunities for science-based applications (Hansen et al. 2013).

In summary, all results obtained in this thesis reveal the importance of an integrated approach in the assessment of fisheries. Concluding remarks are provided in the following section.

8.2 Conclusions

1. This thesis demonstrates the integration of biotic, abiotic and human components to assess recreational fishing effort and harvest using geospatatial methods and under the principles of the ecosystem approach to fisheries (EAF).
2. The development of a low-cost drop-camera system allowed the monitoring of benthic habitats across large areas. The prototype was successful in overcoming the difficulties for obtaining standardized vertical images (i.e., same angle, same height from the seabottom), which allowed obtaining estimates of seagrass cover and occurrence.
3. Empirical spatial models allowed predicting occurrence and cover of seagrass meadows of *Posidonia oceanica* as a function of depth, near-bottom orbital velocities and Landsat derived products. In turn, seagrass meadows have a key role in the essential fish habitat (EFH) of littoral fish populations, providing a valuable ecosystem service to nearshore fisheries and recreational activities. Therefore, information on benthic habitats should need to be incorporated into fisheries management and marine spatial plans.
4. Estimation of home ranges and site fidelity of *S. scriba* and *D. annularis* suggests the potential use of MPAs for protecting adult stocks and the sustainable development of the fishery. Similarly to other target species, they could be used as bioindicators for assessing local exposure to environmental factors and human-induced impacts (e.g., fishing overexploitation).
5. Fishing quality was spatially heterogeneous and could be predicted as function of multiple biophysical parameters together with information on angler-related factors. Future research should be directed toward segmenting recreational anglers in function of their consumptive orientation profiles and preferences.
6. Quantitative response of angler behaviour to multiple attributes was subject to non-linearities, complex interactions and threshold effects. Angler occurrence was mainly related to accessibility, weather conditions, and social factors like business days.
7. Total harvest estimates indicate that the exploitation of the recreational fishery is not negligible, and could be of the same order of magnitude than artisanal fisheries for some fish communities. Therefore, fisheries management should consider this activity under the precautionary approach to support its sustainable development.
8. Species distribution models, supported by computational methods, allowed the modeling of the spatial distribution of habitats, fish and fishers. They provided uncertainty estimates that could be incorporated in science-based tools for supporting the ecosystem approach to fisheries.

Appendix A Sample images with BBCA scores



Appendix B Hierarchical modeling workflow

General approach

The workflow used for the spatial hierarchical models (Chapter 2 and Chapter 3) can be summarized in 8 different steps. They are all sequential, and some of them (Step 3 and Step6) can be considered as optional. For example, the *predictive process approach* (Step 3) was only implemented in Chapter 3 due to the big amount of samples. On the other hand, model selection (Step 6) was not carried out in Chapter 2, similarly to (Latimer et al. 2009). Differences in the implementations between Chapters are presented in Table B.1.

Table B.1 Comparison between the hierarchical models implemented in Chapter 2 and Chapter 3.

Step	Chapter 2	Chapter 3
1. Model specification	y_i varies between 0 and 1	y_i is 0 or 1
2. Distance-based correlation function	Exponential model	Exponential model
3. Predictive process approach	No implemented	Used to overcome "big-n problem"
4. Priors assignment	a_ϕ = 4.80e-4 b_ϕ = 1.60e-2	a_ϕ = 3.02e-4 b_ϕ = 5.96e-2
5. Markov Chain Monte Carlo methods	Number of chains = 3 Iterations per chain = 5,000 Thinning steps = 10 iterations Mixing of the chains = 3,000 Samples retained = 6,000	Number of chains = 3 Iterations per chain = 15,000 Thinning steps = 10 iterations Mixing of the chains = 10,000 Samples retained = 15,000
6. Model selection	No used (3 explanatory variables)	DIC criterion (6 explanatory variables)
7. Cross-validation	RMSE	AUC
8. Sampling the posterior distribution	Grid resolution = 75 x 75 m Post burn-in samples = 950	Grid resolution = 150 x 150 m Post burn-in samples = 500

Step 1. Model specification

A basic formulation of a spatial regression model is the following (Latimer et al. 2009):

$$y_i = x_i\beta + w_i\,, \qquad \text{(Equation B.1)}$$

where $i \in [1,\ldots,n]$ indexes the sampling locations, and the response variable y_i depends on the covariates x_i, the regression slope parameters β, and the vector of errors w_i. We implemented a generalized linear spatial process model, where the response y_i varied from 0 to 1. Then, y_i is modeled through a logistic link regression (Finley et al. 2008) as follows:

$$p(s_i) = \frac{\exp(x(s_i)^T \beta + w(s_i))}{1 + \exp(x(s_i)^T \beta + w(s_i))} \quad \text{(Equation B.2)}$$

where S $\in$ [s_1,…,s_n] indexes locations that are spatially-explicit referenced (i.e., east-north). The vector of errors (W) follows a multivariate Gaussian distribution MVN(0, Σ) (Banerjee et al. 2004, Finley et al. 2008, Latimer et al. 2009).

Step 2. Distance-based correlation function

The variance-covariance matrix Σ incorporates spatial dependence between observations, which is represented as a function (H) of the distance between pairs of points (δ_{ij}). We defined H as an exponential correlation function (Finley et al. 2008, Latimer et al. 2009) that has two parameters associated with it: the spatial decay parameter (ϕ) and the spatial effect variance (σ^2). The exponential correlation between pairs of points is $H(\delta_{ij}) = exp(-\phi\delta_{ij})$. Then, the covariance matrix is defined as $\Sigma_{ij} = \sigma^2 exp(-\phi\delta_{ij})$, where $i,j \in [1,\ldots,n]$. The *effective range* δ_0 in the exponential model is defined as the distance at which the correlation has dropped to 0.05. Thus, if we set $\exp(-\phi\delta_0) = 0.05$, we obtain $\delta_0 \approx 3/\phi$, because $\ln(0.05) \approx -3$ (Banerjee et al. 2004).

Step 3. Predictive process approach

The "big N problem" in spatial statistics is a common constrain when fitting the model to a large number of data (e.g., 1000 points), which requires obtaining the inverse of the dense covariance matrix Σ. As the number of locations n increases, the number of computations to invert Σ increases exponentially at every iteration of the MCMC algorithm. The *predictive process* approach (Banerjee et al. 2008, Latimer et al. 2009) aims to maintain the richness of the hierarchical model specification in the presence of large datasets by speeding the computation. To achieve this, the predictive process reduces the dimension of Σ introducing a second stage to the model, which projects the original process to a smaller number of representative locations $m < n$, called 'knots'. Selection of the sites that will acts as 'knots', can be defined through a spatial-covering design. In our study, 'knot' locations (m = 100) were chosen using a k-means algorithm (i.e., *kmeans* function in R) on the observed locations, which aims to partition the points into k groups such that the sum of squares from points to the assigned cluster centres is minimized.

The link between W^* and W is done through prediction (similar to kriging), where the values of n spatial random effects (W) are predicted from the m values of the predictive process (W^*) (Latimer et al. 2009). A cross-covariance matrix between W and W^* is used to describe the spatial relationship between the m knots and the n locations. This prediction is integrated into the model, allowing the propagation of the associated uncertainty to the first dimensional stage of the model.

Step 4. Priors assignment

We completed the Bayesian hierarchical specification by assigning prior distributions to the model parameters. We assigned a flat prior to the intercept and slope parameters β. The prior distributions for the remaining parameters were consistent with Finley et al. (2008). The variance term σ^2 received an inverse-Gamma prior IG(2, b_σ), with nearly infinite variance and mean determined by b_σ. The latter parameter was the value of the sill (i.e., the asymptotic variance of a spatially autocorrelated process), which was

determined by the empirical variogram of the non-spatial GLM residuals. The spatial decay received a Uniform prior, $\phi \sim U(a_\phi, b_\phi)$. In Chapter 2, a_ϕ = 4.80e-4 and b_ϕ = 1.60e-2, which represents an effective spatial range of 188-6250 m: the minimum and half of the maximum intersite distances. In Chapter 3, a_ϕ = 3.02e-4 and b_ϕ = 5.96e-2, representing an effective spatial range of 50-9911 m.

Step 5. Markov Chain Monte Carlo methods

We fitted the model using Markov Chain Monte Carlo (MCMC) methods with an adaptive Metropolis and the Gibbs algorithm to update all of the parameters (Rosenthal 2007). We ran three independent MCMC chains. In Chapter 2 they contained 5,000 iterations (50,000 samples at thinning steps of 10 iterations); whereas in Chapter 3 they contained 15,000 iterations (150,000 samples at thinning steps of 10 iterations). Each chain was initialized with randomly chosen starting values sampled within a feasible range. We used the CODA package to diagnose the convergence of chains by Gelman-Rubin diagnostics and to assess chain autocorrelations. In Chapter 2, reasonable mixing of the chains was accomplished after 3,000 iterations, so we retained the remaining 6,000 samples (2,000 x 3) to estimate posterior distributions of the parameters. In Chapter 3, mixing of the chains was accomplished at 10,000 iterations, so we retained the remaining 15,000 samples (5,000 x 3).

Step 6. Model selection

We fitted 21 competing models with different combination of covariates. To compare alternative models, we used the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002). The DIC is the sum of the Bayesian deviance (a measure of the model fit) and the "effective" number of parameters (pD, a penalty for the model complexity). Similarly to Akaike Information Criterion (AIC), lower DIC values suggest best fit models.

Step 7. Cross-validation (CV)

CV with RMSE (Chapter 2)

To assess the predictive performance of the model, we held out a randomly selected subset of 15% (n = 10 locations), for cross-validation. We then used the prediction on the random set-aside subset to measure the prediction error of the model (i.e., the cross-validated prediction error). We computed the root mean square error (RMSE). Finally, we also computed the RMSE for a non-spatial logistic regression on a generalized linear model, to compare the two models.

CV with AUC (Chapter 3)

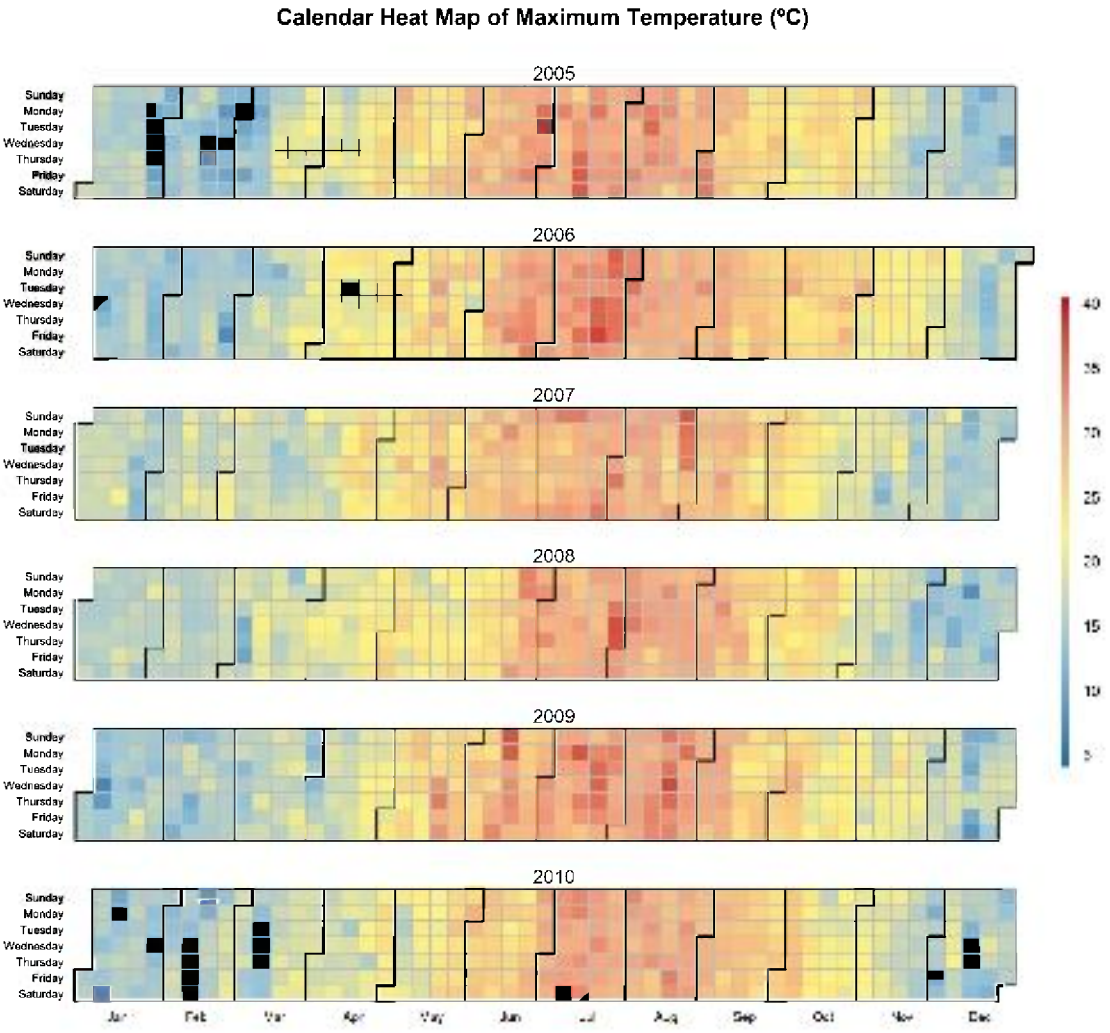
In order to asses the predictive performance of the model we held out a randomly selected subset of 15% (n = 129 locations), for cross-validation. Model quality was quantified using the area under the curve (AUC, PresenceAbsence package) using the computed model predictions on the testing dataset. AUC is a graphical method that assesses the ability of a model to predict the absence or presence of species on the basis of given criteria (e.g. climate variables), by representing the relationship between the false positive fraction and the true positive fraction of the related confusion matrix of the evaluated model (Fielding and Bell 1997). The range of AUC is from 0 to 1. A model providing excellent prediction has an AUC higher than 0.9, a fair model has an AUC between 0.7 and 0.9, and a model is considered as poor if its

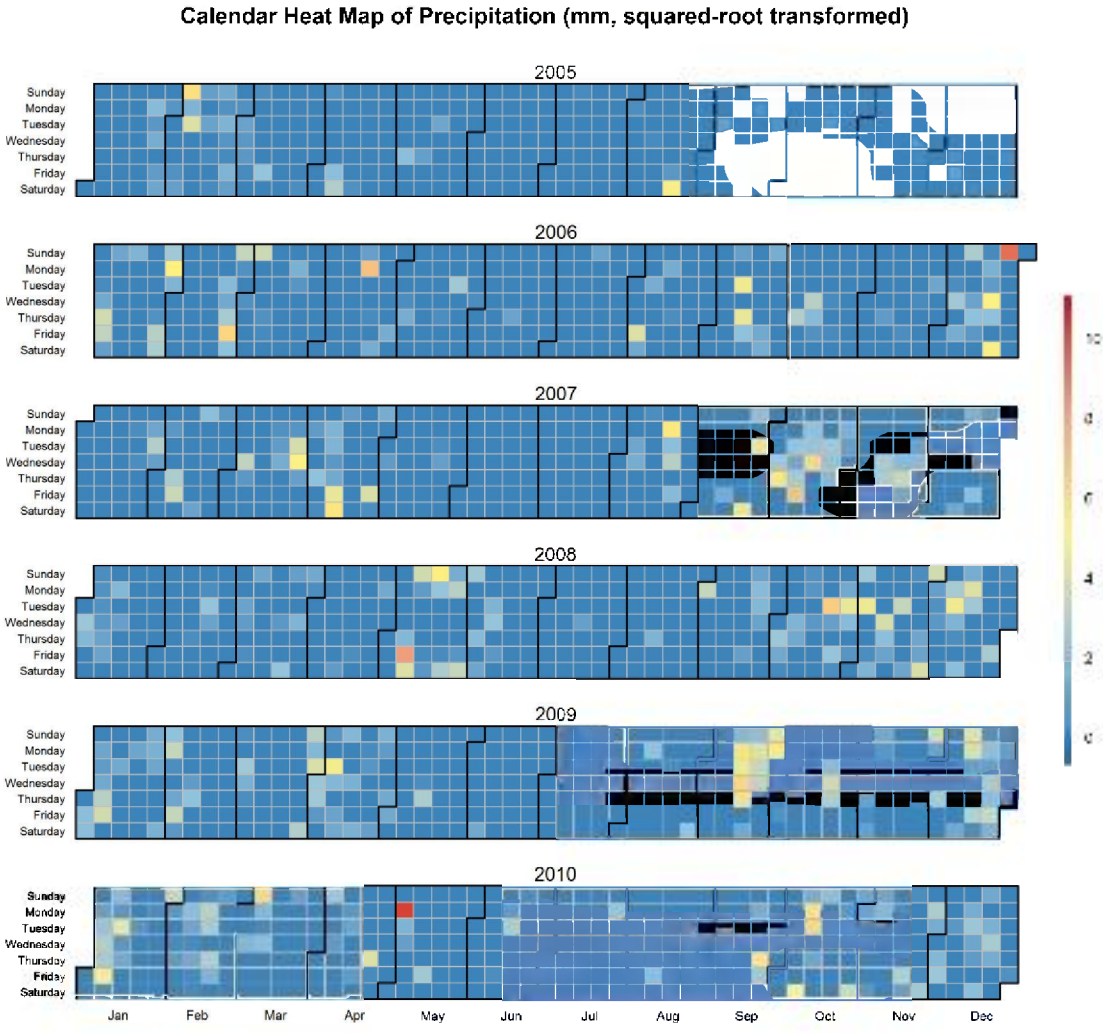
AUC is below 0.7 (Swets 1988). In addition, we used an optimization method to select the threshold that maximized Kappa (Freeman and Moisen 2008). Such threshold was then used to classify probabilities between presence or absence an estimate the extension of the seagrass meadow in the study area.

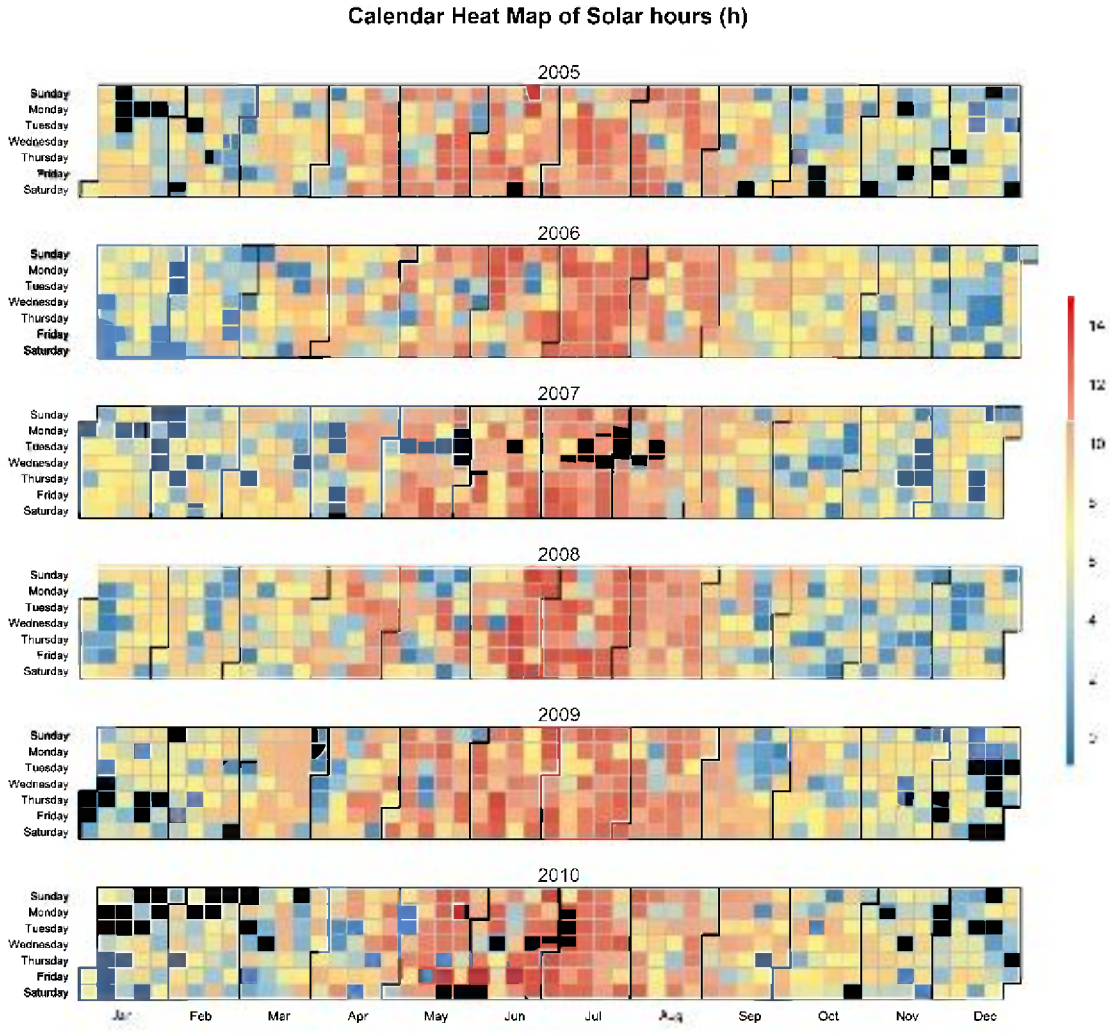
Step 8. Sampling the posterior distribution

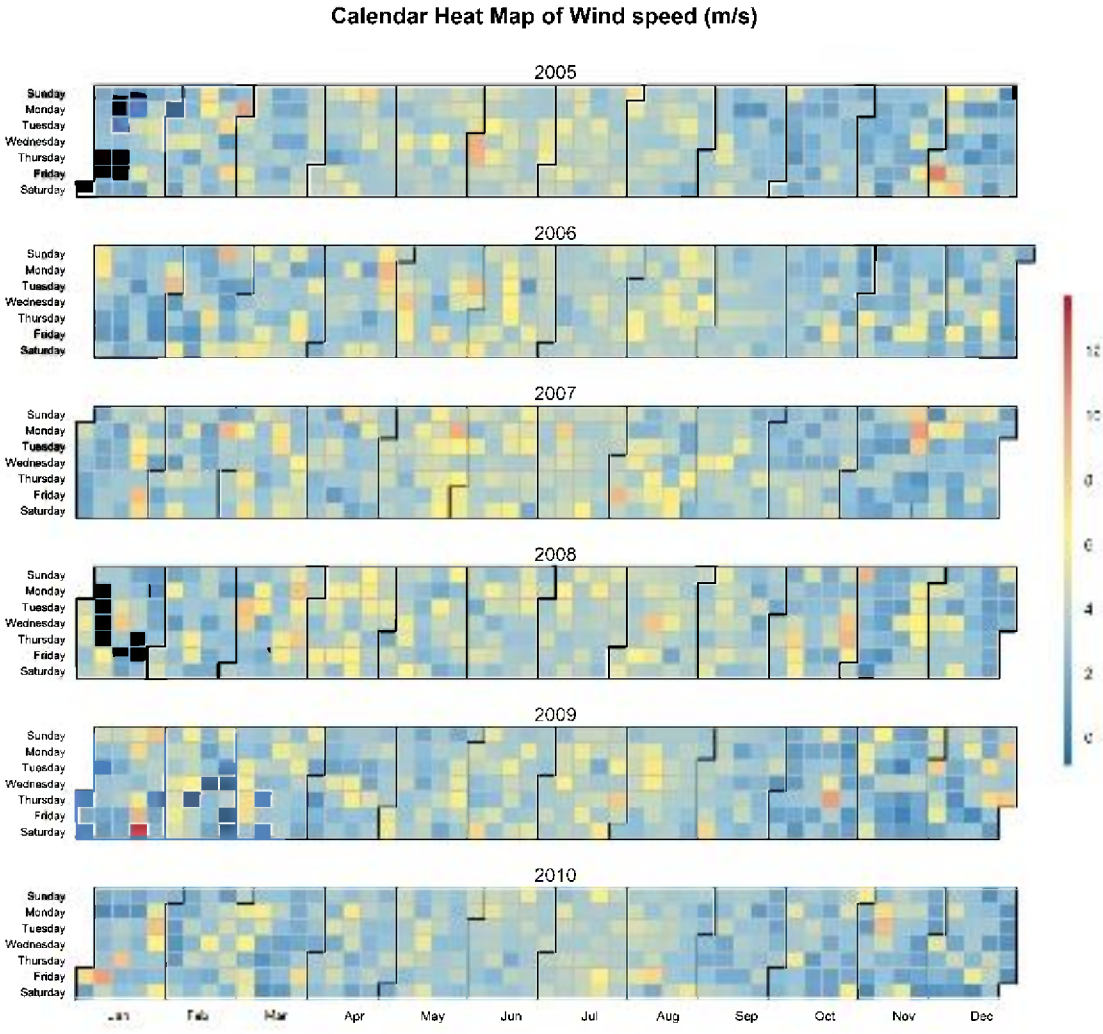
For model prediction at the study area, we resized the spatial resolution of original spatial covariates to a resolution size of 75 x 75 m (Chapter 2), or 150 x 150 m in the case of Chapter 3 due to computation time constraints. Given the samples from the parameters' posterior distribution of the selected model, we also sampled from the posterior predictive distribution of every pixel across the study area. In the case of Chapter 2, the study area was defined by the presence of *P. oceanica* determined by the Posidonia-LIFE map. Predictions were based on 950 samples (Chapter 2) or 500 samples (Chapter 3) of the post burning and thinned posterior distribution. We created a probability surface of seagrass cover (Chapter 2) or coverage (Chapter 3) using the posterior median, and an uncertainty map using the 95% credible interval width (i.e., the range between the 0.025 and 0.975 quantiles).

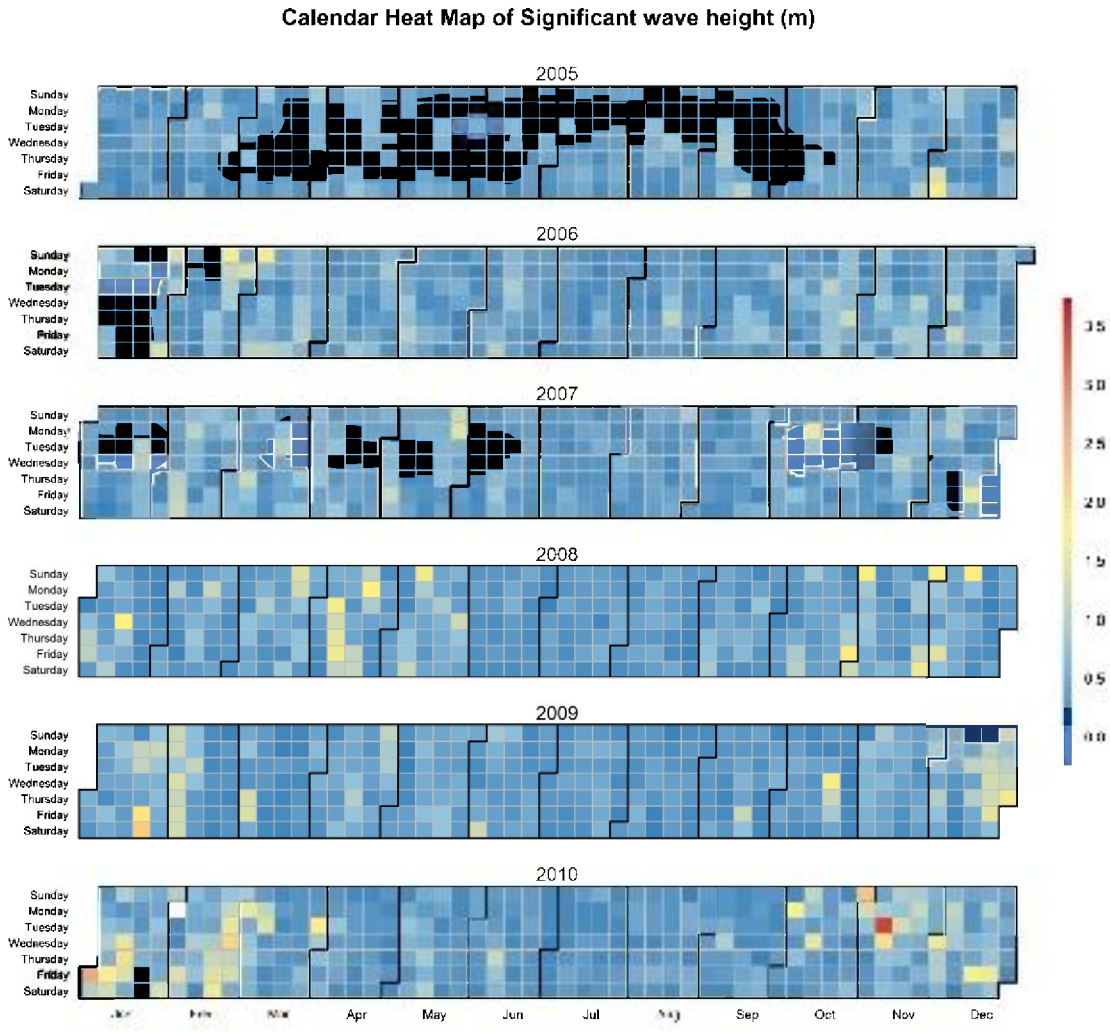
Appendix C Temporal variables used for fitting the BRT

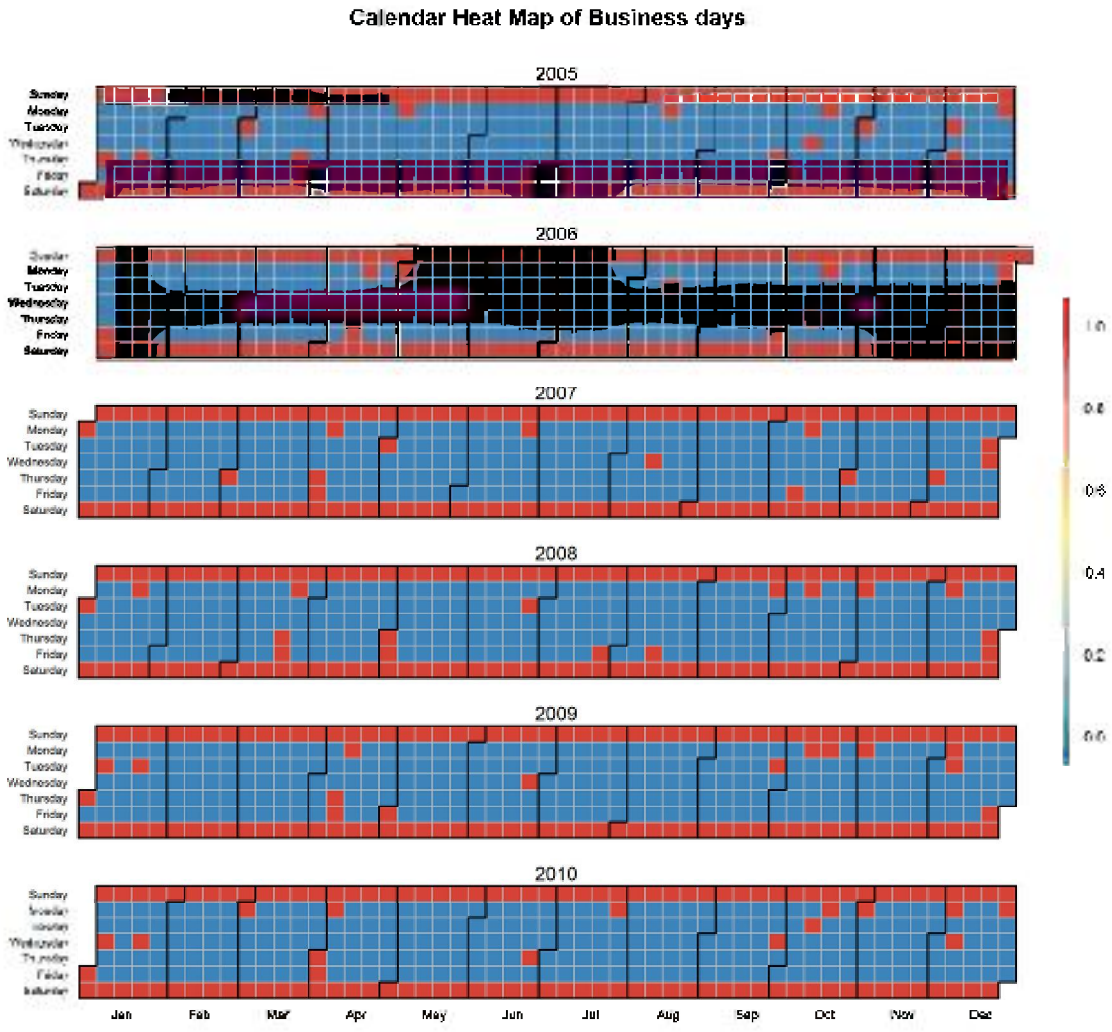



Calendar Heat Map of Precipitation (mm, squared-root transformed)
2005
2006
2007
2008
2009
2010
Sunday
Monday
Tuesday
Wednesday
Thursday
Friday
Saturday
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec


Calendar Heat Map of Solar hours (h)
2005
2006
2007
2008
2009
2010
Sunday
Monday
Tuesday
Wednesday
Thursday
Friday
Saturday
Jan
Feb
Mar
Apr
May
Jun
Jul
Sep
Oct
Nov
Dec
14
12


Calendar Heat Map of Wind speed (m/s)
2005
2006
2007
2008
2009
2010
Sunday
Monday
Tuesday
Wednesday
Thursday
Friday
Saturday
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec


Calendar Heat Map of Significant wave height (m)
2005
2006
2007
2008
2009
2010
Sunday
Monday
Tuesday
Wednesday
Thursday
Friday
Saturday
Apr
May
Jun
Jul
Sep
Oct
Nov
Dec
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0


Calendar Heat Map of Business days
2005
2006
2007
2008
2009
2010
Sunday
Monday
Tuesday
Wednesday
Thursday
Friday
Saturday
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Appendix D Supplementary results of BRT models

Table D1. Fitted combinations of the binomial part for model optimization. Results are ordered by predicted deviance. Selected parameters for analysis are marked in bold.

Learning rate	Tree complexity	Bag fraction	Num. of trees	Deviance
0.005	**5**	**0.6**	**2350**	**0.3780**
0.01	5	0.6	1400	0.3780
0.01	3	0.7	1850	0.3780
0.005	5	0.7	2400	0.3784
0.005	5	0.5	2400	0.3784
0.005	3	0.5	3750	0.3786
0.01	5	0.5	1300	0.3787
0.01	1	0.5	3300	0.3788
0.005	3	0.7	3300	0.3790
0.005	3	0.6	3000	0.3790
0.01	5	0.7	1600	0.3790
0.001	5	0.6	7600	0.3791
0.01	1	0.6	3100	0.3791
0.01	3	0.6	1800	0.3793
0.01	3	0.5	1950	0.3794
0.005	1	0.5	5050	0.3795
0.01	1	0.7	3400	0.3795
0.001	5	0.5	6950	0.3796
0.001	5	0.7	7100	0.3798
0.005	1	0.6	5200	0.3799
0.005	1	0.7	5000	0.3805
0.001	3	0.6	8750	0.3809
0.0005	5	0.5	11150	0.3809
0.0005	5	0.7	11050	0.3810
0.001	3	0.7	8700	0.3811
0.0005	5	0.6	11000	0.3811
0.001	3	0.5	8550	0.3811
0.0005	3	0.7	13000	0.3829
0.0005	3	0.5	12700	0.3830
0.001	1	0.7	13600	0.3836
0.0005	3	0.6	12100	0.3837
0.001	1	0.5	12300	0.3840
0.001	1	0.6	12700	0.3840
0.0005	1	0.6	15000	0.3899
0.0005	1	0.5	15000	0.3899
0.0005	1	0.7	15000	0.3900

Table D2. Fitted combinations of the Poisson part for model optimization. Results are ordered by predicted deviance. Selected parameters for analysis are marked in bold.

Learning rate	Tree complexity	Bag fraction	Num. of trees	Deviance
0.005	5	0.7	1650	0.516
0.001	**5**	**0.7**	**5250**	**0.517**
0.01	5	0.7	850	0.518
0.01	5	0.5	1200	0.519
0.0005	5	0.7	7850	0.519
0.005	5	0.5	1200	0.519
0.0005	5	0.6	8250	0.519
0.005	5	0.6	1550	0.520
0.001	5	0.6	4900	0.520
0.01	3	0.7	1450	0.520
0.001	5	0.5	3950	0.523
0.005	3	0.7	2250	0.523
0.01	5	0.6	950	0.523
0.001	3	0.7	7900	0.524
0.0005	5	0.5	7050	0.525
0.005	3	0.6	2400	0.525
0.01	3	0.6	1300	0.525
0.0005	3	0.7	11650	0.526
0.001	3	0.6	6250	0.527
0.005	3	0.5	1750	0.529
0.001	3	0.5	5950	0.529
0.01	3	0.5	1050	0.530
0.0005	3	0.6	9600	0.530
0.0005	3	0.5	8650	0.533
0.01	1	0.7	3050	0.536
0.005	1	0.7	4850	0.538
0.001	1	0.7	13300	0.546
0.01	1	0.6	2300	0.549
0.005	1	0.6	3100	0.549
0.01	1	0.5	2350	0.551
0.005	1	0.5	3650	0.553
0.001	1	0.6	9250	0.556
0.0005	1	0.7	15000	0.556
0.0005	1	0.6	15000	0.559
0.001	1	0.5	9350	0.559
0.0005	1	0.5	11300	0.567

Table D3. Relative strength of interactions between predictor variables for the binomial part. Top five interactions are marked in bold.

	Depth	dNat	dCoast	dPort	Rock	Seagrass	Cpue	Ypue	MLt	Shan	busD	Tmax	Wmed	Prec	Sun	Hm0	Morning	year	month	MPA
Depth	0	0	0.11	0.05	0	0	0.01	0.3	0.14	0.02	0.04	0.16	0.12	0	0	0.09	0	0.01	0	0
dNat	0	0	0	0.82	0.02	0	0.11	0.56	0.85	0.12	0.54	0.92	0	0.02	0.01	0.09	0.06	2.07	0	0.24
dCoast	0	0	0	9.9	0.01	0	0.56	1.87	10.25	0.07	0.03	2.65	0.08	0.01	0	0.27	0.13	0.72	0	0
dPort	0	0	0	0	0.65	0.01	0.63	0.11	1.98	3.29	**26.75**	**18.41**	7.02	0.74	0.73	**30.63**	**37.12**	8.43	0.09	0.02
Rock	0	0	0	0	0	0	0.08	0	0.02	0.01	0	0.07	0.54	0.01	0.09	0.01	0.01	1.57	0.01	0
Seagrass	0	0	0	0	0	0	0	0.01	0.07	7.62	0.04	0.31	0.04	0	0	0.03	0.02	0.05	0	0
Cpue	0	0	0	0	0	0	0	0.94	7.08	9.45	0.16	0.36	0.78	0	6.4	0.18	0.04	8.8	5.73	0.03
Ypue	0	0	0	0	0	0	0	0	2.05	0.1	0.09	0.48	0.11	0.01	0.09	0.55	0.28	0.07	0.03	0
MLt	0	0	0	0	0	0	0	0	0	0.61	0.13	2.61	4.21	0.02	0.11	0.08	0.13	0.41	0.04	0.01
Shan	0	0	0	0	0	0	0	0	0	0	0.55	8.97	2.08	0.03	0.05	0.19	0.15	0.14	1.88	0.11
busD	0	0	0	0	0	0	0	0	0	0	0	0.34	0	0.16	0	5.95	0.1	0	0	0.43
Tmax	0	0	0	0	0	0	0	0	0	0	0	0	0.03	0.01	0.09	0.19	0.23	2.19	0.01	0.77
Wmed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.08	0.03	0.28	0.01	0	0.04
Prec	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	1.2	0	0	0.06
Sun	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0.01	0	0
Hm0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**17.14**	0.01	0	0.45
Morning	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	1.33
year	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.01
month	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MPA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D4. Relative strength of interactions between predictor variables for the Poisson part. Top five interactions are marked in bold.

	Depth	dNat	dCoast	dPort	Rock	Seagrass	Cpue	Ypue	MLt	Shan	busD	Tmax	Wmed	Prec	Sun	Hm0	Morning	year	month	MPA
Depth	0	0	0.14	**0.88**	0	**0.91**	0	0.01	0.02	0.02	0	0.02	0.03	0	0.01	0.22	0	0	0	0
dNat	0	0	0	0.01	0	0	0	0	0	0	0	0.01	0.02	0	0.22	0	0	0	0	0
dCoast	0	0	0	0.13	0	0.13	0	0.01	0.01	0	0	0	0	0	0.03	0.01	0	0	0	0
dPort	0	0	0	0	0.01	**0.61**	0.21	**0.5**	0.03	0.01	0	0.01	0.11	0	**0.71**	0.05	0	0.07	0.01	0
Rock	0	0	0	0	0	0.01	0	0	0.01	0	0	0	0.04	0	0	0	0	0.01	0	0
Seagrass	0	0	0	0	0	0	0	0.16	0.01	0	0	0.01	0.13	0	0.07	0	0	0.04	0	0
Cpue	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0.07	0	0	0	0	0
Ypue	0	0	0	0	0	0	0	0	0.03	0.01	0	0.02	0.01	0	0.03	0.01	0	0	0	0
MLt	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0.01	0.06	0	0.01	0	0
Shan	0	0	0	0	0	0	0	0	0	0	0	0.01	0.06	0	0.07	0.01	0	0	0	0.01
busD	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tmax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.03	0	0
Wmed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.02	0	0.15	0	0
Prec	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sun	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0
Hm0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Morning	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
year	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
month	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MPA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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